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Volume 116
Number 2
April 2018

Fishery Bulletin

Contents

Articles

111–125 **Kiyomi J. French, Nancy L. Shackell, and Cornelia E. den Heyer**

Strong relationship between commercial catch of adult Atlantic halibut (*Hippoglossus hippoglossus*) and availability of suitable habitat for juveniles in the Northwest Atlantic Ocean

126–141 **Noëlle Yochum, Allan W. Stoner, David B. Sampson, and Craig Rose**

A comparison of laboratory-holding and tag-return methods for evaluating delayed mortality of Dungeness crab (*Cancer magister*) discarded in Oregon fisheries

142–152 **Daniel M. Weaver, Stephen M. Coghlan Jr., and Joseph Zydlewski**

The influence of nutrients from carcasses of sea lamprey (*Petromyzon marinus*) on larval growth and spawner abundance

Short contribution

153–160 **Kristina Zhukova, Olga A. Maznikova, and Alexei M. Orlov**

Gonadal maturation of the female smooth lumpsucker (*Aptocyclus ventricosus*)

Articles

161–170 **Abigail S. Clark, Steven H. Jury, Jason S. Goldstein, Thomas G. Langley, and Winsor H. Watson III**

Underwater video surveillance of American lobsters (*Homarus americanus*) to understand saturation levels in lobster traps

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The NMFS Scientific Publications Office is not responsible for the contents of the articles.

171–182 Hui-Yu Wang and Mikko Heino

Adaptive and plastic variation in growth and maturation of the cutlassfish *Trichiurus japonicus* in the subtropical Pacific Ocean

Short contribution

183–189 Hakan Ayyildiz and Aytac Altin

Age and growth rates at the early life stages of common Pandora (*Pagellus erythrinus*) based on analysis of otolith microstructure

Article

190–206 Chantel R. Wetzel, André E. Punt, and Jason M. Cope

The effect of reduced data on the ability to monitor rebuilding of overfished fish stocks

Short contribution

207–214 Gerald L. Crow, Bradley M. Wetherbee, Robert L. Humphreys Jr., and Richard Young

Vertical distribution, diet, and reproduction of the velvet dogfish (*Zameus squamulosus*) in waters off Hawaii

215–218 Guidelines for authors

National Marine Fisheries Service
NOAA

Fishery Bulletin
established in 1881

Spencer F. Baird
First U.S. Commissioner of Fisheries and founder of *Fishery Bulletin*

Strong relationship between commercial catch of adult Atlantic halibut (*Hippoglossus hippoglossus*) and availability of suitable habitat for juveniles in the Northwest Atlantic Ocean

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Abstract—Atlantic halibut (*Hippoglossus hippoglossus*) is an increasingly valued commercial fish and its recent population growth has attracted the attention of fisheries scientists and managers both within and outside Canada. With renewed transnational interests in this species, fishery managers have relied on existing, but limited, ecological information for multilateral discussions on shared allocations of catch. To address this dearth of information, we modeled species distribution using maximum entropy, where by survey catch data were related to environmental data to quantify habitat suitability. We then calculated the amount of suitable habitat for juvenile Atlantic halibut per Northwest Atlantic Fisheries Organization (NAFO) divisions, within and outside Canada's Exclusive Economic Zone. Among NAFO divisions, we found a strong relationship between the availability of suitable habitat for juvenile Atlantic halibut, and both current and historical fisheries landings. Results are consistent with the nursery-size hypothesis which states that the amount of available juvenile habitat is related to the level of adult production. The majority of occupied suitable habitat is found on the southwestern half of Canada's Scotian Shelf, whereas the U.S. and international waters off Newfoundland have ample suitable habitat to support larger populations. Quantifying habitat suitability and linking this suitability to stock abundance and distribution is an important step toward an ecosystem approach for the management of Atlantic halibut.

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In the Northwest Atlantic Ocean, Atlantic halibut (*Hippoglossus hippoglossus*) range from Greenland to Virginia, United States (Bigelow and Schroeder, 1953; Collette and Klein-MacPhee, 2002). In Canada, it is currently managed as 2 stocks. The larger stock, which is the subject of this article, extends from the Southern Grand Banks of Newfoundland, across the Scotian Shelf, and into the Gulf of Maine (Fig. 1). The stock ranges over multiple North Atlantic Fisheries Organization (NAFO) divisions and, importantly, spills over international boundaries into the territorial waters of the United States, Overseas France, and the international High Seas regulatory area. Despite a history of overfishing (Grasso, 2008), Canadian assessments show that the stock has rebounded in the last decade, is benefiting from a period of high recruitment (DFO[1,2];Trzcinski and Bowen, 2016), and was the third most valuable groundfish in Canada in 2015 (Economic Analysis and Statistics, Department of Fisheries and Oceans Canada, landings data, available from website). The Canadian fishery is now certified "sustainable" by the Marine Stewardship Council (Marine Stewardship Council, Track a Fishery, website). In contrast, under the U.S. Endangered Species Act, Atlantic halibut is listed as a "Species of Concern" from Labrador, Canada, to southern New England (USA) (NOAA[3]), and the 2015 results of the U.S. halibut assessment model were rejected owing to limited information (an action that has enforced the view that the stock is still in an overfished state) (Hennen[4]).

[1] DFO (Department of Fisheries and Oceans Canada). 2015. 2014 assessment of Atlantic halibut on the Scotian Shelf and southern Grad Banks (NAFO Divisions 3NOPs4VWX5Zc). Can. Sci. Advis. Secr. Sci. Advis. Rep. 2015/012, 16 p. [Available from website.]

[2] DFO (Department of Fisheries and Oceans Canada). 2015. Stock Assessment of Atlantic Halibut of the Gulf of St. Lawrence (NAFO Divisions 4RST) for 2013 and 2014. Can. Sci. Advis. Secr. Sci. Advis. Rep. 2015/023, 15 p. [Available from website.]

[3] NOAA. 2013. Species of concern: Atlantic halibut, 2 p. [Available from website.]

[4] Hennen, D. 2015. Atlantic halibut. *In* Operational assessment of 20 Northeast groundfish stocks, updated through 2014. U.S. Dep. Commer., Northeast. Fish. Sci. Cent. Ref. Doc. 15-14, p. 171–179. [Available at website.]

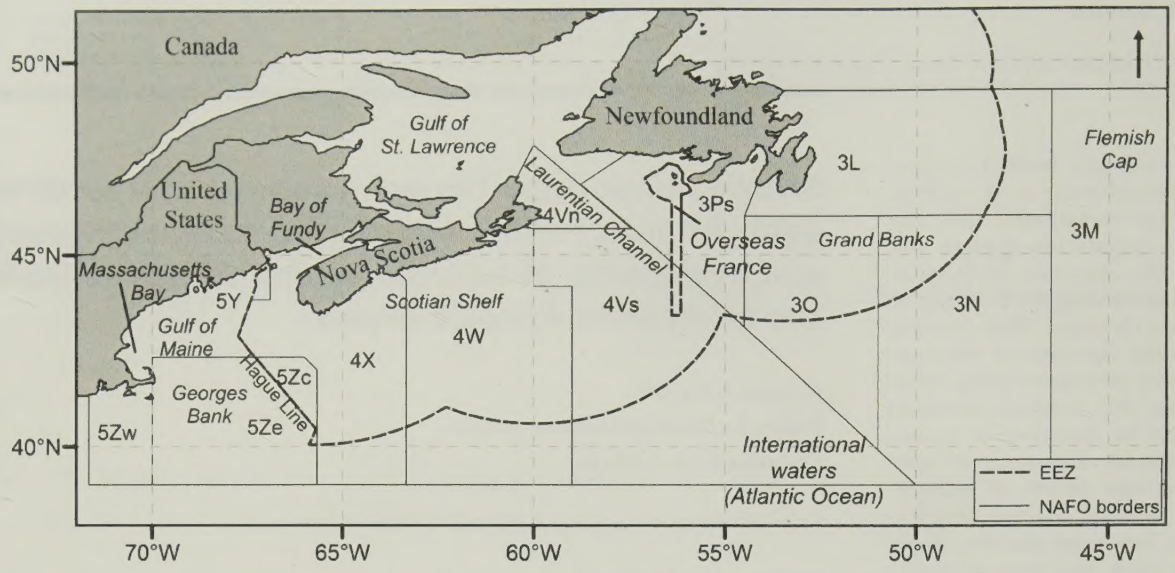

Figure 1

Map of the range of the stock of Atlantic halibut *(Hippoglossus hippoglossus)* on the Scotian Shelf and southern Grand Banks, and areas of interest for this study in which the relationship between commercial catch of adult Atlantic halibut and availability of suitable habitat for juveniles in the northwest Atlantic Ocean was examined (by using data from surveys conducted during 2001–2013 and maximum entropy modeling). Thin, solid lines indicate the borders of North Atlantic Fisheries Organization (NAFO) divisions, within and outside of Canada's Exclusive Economic Zone (EEZ).

Informal reports from both the U.S. and French fishing industries suggest that halibut are becoming more abundant within their jurisdictions and fishery managers have expressed renewed commercial interest in the Atlantic halibut fishery. However, there is limited ecological information to support transnational discussions concerning shared allocations of catch (Bigelow and Schroeder, 1953; McCracken, 1958; Stobo et al., 1988; Neilson et al., 1993; Cargnelli et al., 1999). A major challenge facing Atlantic halibut research is a lack of data on the past and present distributions and abundances of this species. Historically this species became of commercial interest only after decades as discarded bycatch in the cod (*Gadus morhua*) fishery and was quickly exploited to a critical state in the 1850s (Grasso, 2008). Before the establishment of a fishery-independent index of abundance (1970s), Atlantic halibut were heavily impacted by fishing activity for other groundfish, and the current period of high recruitment especially in Canada, is a relative measure compared with abundances during the regional groundfish moratorium of the early 1990s (Collette and Klein-MacPhee, 2002; Grasso, 2008).

Atlantic halibut is the largest of all flatfish (Bigelow and Schroeder, 1953; Collette and Klein-MacPhee, 2002). It is long lived and sexually dimorphic; males reach maturity at smaller sizes (77–80 cm in total length [TL]) than females (103–125 cm TL) (Bowering, 1986; Trumble et al., 1994; Sigourney et al., 2006). This species is capable of long-distanced migrations, but the majority of tagged fish are recaptured locally (McCracken, 1958; Jensen and Wise, 1961; Neilson et al.[5]; Stobo et al., 1988; Kanwit, 2007; den Heyer et al., 2012; Seitz et al., 2016) and therefore may reflect populations with both resident and migratory individuals (e.g. Nielsen and Seitz, 2017) or seasonal migrations to putative spawning areas (e.g., Le Bris et al., 2017). This finding indicates lower levels of mixing than those under the long-held presumption that the stock is a large, interbreeding population (Seitz et al., 2016). The tendency to remain stationary until the age of 4–6 years and a homing response to spawning grounds have been observed among Atlantic halibut in Norway (Godø and Haug, 1988). In the Northwest Atlantic, a lack of known spawning-site location and egg or larvae data has meant that distributions of this species during the earliest life history stages are unknown. Moreover, because current standardized trawl surveys are limited by depth, they lead to uncertainties in determining halibut presence and activities in deeper waters. Studies with electronic tags to elucidate northwest migration patterns and spawning locations of Atlantic halibut (e.g. Armsworthy et al., 2014; Seitz et al., 2016; Murphy et al., 2017; Le Bris et al., 2017) will ultimately improve our ability to define and manage halibut stocks. However, owing to growing commercial interests, there is an immediate need for scientific information to support management decisions.

[5] Neilson, J. D., W. R. Bowering, and A. Fréchet. 1987. Management Concerns for Atlantic halibut (*Hippohlossus hippoglossus*) in the Canadian North Atlantlc. CAFSAC Res. Doc. 87/73, 23 p. [Available from website.]

Availability of suitable habitat is the cornerstone of several ecological theories. In particular, the theory of density-dependent habitat selection describes how animals occupy the most suitable habitat first and expand to more marginal habitat when competition for resources in the prime habitat reduces the fitness benefit of that area (Fretwell and Lucas, 1970; MacCall, 1990). In practice, this concept has been documented in multiple marine systems (Swain and Wade, 1993; Marshall and Frank, 1995; Rangeley and Kramer, 1998; Shackell et al., 2005). There is also extensive evidence that range size and abundance of a species are correlated, and that availability of suitable habitat is strongly and positively correlated with total abundance (Gaston and Blackburn, 1996; Brosse et al., 1999; Holbrook et al., 2000; VanDerWal et al., 2009).

Any life history stage is subject to habitat limitation and to the nursery-size hypothesis that stems from the idea that recruitment and adult fish population density can be constrained by the availability of nursery habitat because of density-dependent mortality during juvenile life stages (Iles and Sinclair, 1982; Rijnsdorp et al., 1992; Gibson, 1994; Beverton, 1995). The idea has resurged in the results of recent studies that have shown a solid relationship between availability of nursery habitat and the recruitment of adults (Sundblad et al., 2014; Wilson et al., 2016). It is theorized that because younger fish are likely to have a narrower range of suitable habitat, regardless of how well-defined their nursery grounds are, juvenile habitat falls within a restricted domain of the adult range (Gibson, 1994; Beverton, 1995). To explore this notion, Sundblad et al. (2014) mapped nursery habitat distributions for predatory fish between mainland Finland and Sweden's archipelago region of the Baltic Sea, and found that they can be quantified and used to help estimate potential adult production. Similarly Wilson et al. (2016) added support to the nursery size hypothesis; they found a relationship between increased recruitment and the presence of juvenile flatfish and concluded that accurate predictions of flatfish nursery locations can be useful for population management.

We use these principles to support evidence-based management by quantifying suitable habitat for juvenile Atlantic halibut and relating it to adult landings in directed fisheries. In this article, we expand upon the work of Shackell et al. (2016) who hypothesized that there was ample suitable habitat available in U.S. waters to support a larger juvenile population. We estimate the distribution of suitable juvenile habitat in each NAFO division, within and outside Canada's Exclusive Economic Zone (EEZ). We then express the amount of suitable habitat (SH) per NAFO division as a relative value (SH-based shares: the proportion of the total available suitable habitat that falls within each NAFO division), and show that these values are related to the proportional shares of commercial fishery landings (adult) among NAFO divisions allocated on the basis of total landings of Atlantic halibut (abundance-based shares [landings]). We propose that this relationship can be considered a baseline for expected juvenile and fishery production per NAFO division. We further propose that suitable habitat can be used as a proxy for production in the absence of more detailed ecological information. In areas where the relationship between expected juvenile habitat and fishery productivity substantially stray from a 1:1 relationship, further research is required to understand the mechanisms controlling the population, and to support the spatial management of this fishery.

Material and methods

Modeling species distribution with a correlative approach

Species distribution models are designed to predict the limits of geographic range and habitat suitability for a selected species, by using functions that relate physiological (mechanistic) or distributional (correlative) data to areas of unknown occupancy (Kearney and Porter, 2009; VanDerWal et al., 2009). Maximum entropy is a correlative approach that can be used for modeling species distribution because it describes the relationship between survey (coordinate) and environmental data (raster layers) (Elith et al., 2011). It is commonly used to study the distributions of invasive species, shifts in distribution related to climate change, and the spatial diversity of species (Phillips and Dudik, 2008; Elith et al., 2011; Fitzpatrick et al., 2013).

As it pertains to the model, entropy is a measure of the uncertainty in a data set (Cover and Thomas, 1991); a uniform distribution would represent complete uncertainty. A maximum entropy model uses multimodal logistic regression with information from observational data and maximizing entropy based on environmental constraints (Jaynes, 1957; Elith et al., 2011). The logistic output from this model is a prediction layer that maps the relative habitat suitability of all locations on the basis of prevailing conditions where the species has been observed. From habitat suitability, we can infer the probability of species presence (VanDerWal et al., 2009). The output scales from 0 to 1, where 0.5 represents the relative habitat suitability and probability of presence, where environmental conditions are 'typical for presence' (Phillips et al., 2006; Phillips and Dudik, 2008; Elith et al., 2011; details in Suppl. Material). VanDerWal et al. (2009) found that for many species, a positive relationship exists between habitat suitability and local abundance, and that these models provide useful insights into spatial patterns of abundance.

We chose to model with maximum entropy to take advantage of its ability to accurately predict in unsampled locations, the several parameterizations available to account for biases in the data, and the continuous and common scale of model outputs that enable direct comparison among models (Phillips et al., 2006). Additionally, unlike Shackell et al.'s (2016) use of a generalized additive model for a similar analysis, our method

enabled us to predict across a much larger area, and because the research vessel survey data are zero inflated (absences are less certain than presences among survey data), we were able to take advantage of the presence-only modeling capabilities of maximum entropy (Sundblad et al., 2014).

Data

We modeled habitat suitability by using research survey data from 2001 through 2013—a timeframe that captures the current period of high Atlantic halibut recruitment. The U.S. National Marine Fisheries Service, NOAA, and Fisheries and Oceans Canada (DFO) have conducted seasonal or annual research surveys (or both) to foster an improved understanding of groundfish abundance and distribution since the early 1960s (NOAA) and 1970s (DFO), (Azarovitz, 1981; Simon and Comeau, 1994). The Canadian surveys sample NAFO divisions off Newfoundland and Labrador (NF), Nova Scotia (NS), and within the Northern and Southern Gulf of St. Lawrence (GSL) (Fig. 1). The U.S. surveys sample Georges Banks, the Gulf of Maine, and the Bay of Fundy (here, we collectively refer to these regions as "U.S." (Fig. 1). All surveys were conducted with bottom-trawl gear and fish abundance, biomass, water depth, and bottom temperature were recorded in a comprehensive database, which can be publically accessed from the Ocean Biogeographic Information System (available from website; Shackell et al., 2005; DFO[6]). Since the start of these surveys (~1963), they have been performed during all seasons and 7 different gear types have been used. A wide variety of fish species are captured over the course of each cruise; Atlantic halibut are usually caught as juveniles (annual median fish length 40–50 cm TL), and larger halibut are thought to outswim the trawls (Trzcinski and Bowen, 2016). Samples were collected from all the NAFO divisions of interest, although there are variations in survey seasonality, intensity, and gear type, and there is difficulty in sampling over rough terrain. Because of these limitations and variations between surveys there are unsampled regions throughout the study area (Suppl. Tables 1 and 2) (online only), all of which can produce an uneven and biased data set because some regions have more representative (larger in quantity and more evenly distributed) sample sets than others.

If bias is not accounted for, the predictive power of the model is lessened (Philips and Dudik, 2008). Fourcade et al. (2013) explored 5 parameterizations available to maximum entropy modeling that are commonly used to correct for bias, thus enabling models to predict more accurately in under-sampled locations. These methods include 1) systematic sampling (data are placed on a grid and one random sample per cell is used in analysis), 2) clustering samples (data are subset by using a principal component analysis that identifies spatial autocorrelation), 3) restricting the background (selecting only background points that fall within the extent of the survey [comparable to using locations where surveys yield true absence of fish]), 4) incorporating a bias file (values are weighted by using a raster that reflects the sampling effort or sampling probability), and 5) geographically splitting the data (the model is computed separately for each area and results are combined) (Fourcade et al., 2013). While designing our model, we tested several of these data correction techniques and compared their ability to improve output diagnostics; however we did not attempt to systematically sample or cluster data because this approach would have caused too many data to have been lost.

We incorporated 5 environmental raster layers in our model: 1) bathymetry (created with the GEBCO 30 arc-second grid obtained from the General Bathymetric Chart of the Oceans (available from website), 2) slope (created by calculating percent rise from the GEBCO 30 arc-second grid), 3 and 4) seasonal mean bottom temperatures for summer and winter in degrees Celsius, and 5) the range in mean temperature between summer and winter, at a 0.1° resolution. Temperature data were obtained from the Global Ocean Reanalyses and Simulations (GLORYS; Mercator Ocean, available from website], which describe monthly mean ocean climate conditions at a 1/4° lat.×long. resolution. We chose to work with GLORYS temperature data instead of the data that were collected from the trawl censors because GLORYS provided a complete and uniform coverage of the area that is more conducive to interpolation. We limited our model to 5 predictor variables because the use of excessive variables can lead to overfitting the data (Philips and Dudik, 2008). We selected variables that describe groundfish habitat (the bottom), and variables for which there were data for the entire study area. We interpolated the temperature layers by using ordinary kriging and 2001 through 2011 data. To prepare data for interpolation, we grouped monthly measures by season (summer: July–September, winter: January–March), calculated the mean annual temperatures for each season, and then assigned the 10-year average to each datum point. Finally, we incorporated regional variability in temperature by calculating the annual mean range in temperature by taking the difference of the seasonal means, and averaging these values across the entire sampling period.

We used 3 shapefiles (NAFO, available from website) to spatially classify the study area for spatial comparisons: NAFO boundaries, the EEZ, and the Hague line (Fig. 1). The waters stretching from the northern limits of Baffin Island to Cape Hatteras are known as the NAFO Convention Area, which is divided into subareas, divisions, and subdivisions (Halliday and Pinhorn, 1990). Although some of the areas of interest are formally referred to as "subdivisions," we refer to all areas as "NAFO divisions" throughout this analysis. We

[6] DFO (Department of Fisheries and Oceans Canada). 2016. 2015 Maritimes research vessel survey trends on the Scotian Shelf and Bay of Fundy. Can. Sci. Advis. Secr. Sci. Resp. 2016/011, 66 p. [Available from website.]

Table 1

The 4 models of species distribution used to test different combinations of parameterization techniques used, in turn, to correct data biases in this study of the relationship between commercial catch of adult Atlantic halibut (*Hippoglossus hippoglossus*) and availability of suitable habitat for juveniles in the northwest Atlantic Ocean. Correction parameters are those outlined by Fourcade et al. (2013). Cross-validation produced values for the area under the omission curve (AUC), which indicate a model's proficiency in differentiating between presence and absence sites.

Correction parameters	Method	AUC
Default		0.83
Restricted background	Select only background points that fall within the extent of the survey: use true absence locations	0.81
Restricted background + bias file	Select only background points that fall within the extent of the survey: use true absence locations + weight values by incorporating the raster layer that reflects the sampling effort or sampling probability	0.80
Restricted background + split	Select only background points that fall within the extent of the survey: use true absence locations + geographically splitting the data, compute the model separately for each area, then combine results	0.89 (mean)

subset the NAFO shapefile to include only the divisions that represent the extent of the Southern Grand Banks and Scotian Shelf stock. The NAFO Convention Area was further subdivided by 1) the Canadian EEZ, which is drawn 370 km (200 nautical mi) from shore to mark the extent of national jurisdiction over waters and the beginning of shared international resources, and 2) the Hague line, which delineates the border between waters of Canada and the United States (Halliday and Pinhorn, 1990; Anderson, 1998) (Fig. 1).

To measure adult abundance of Atlantic halibut, we used 3 data sets from the Atlantic halibut fishery. For recent values, we used commercial landings by division from 2010 through 2014 (DFO, seafisheries landings, available from website); these data reflect both data from directed fisheries and data on bycatch. We also used Butler and Coffen-Smout's (2017) map of landings, by catch weight, to spatially represent the MARFIS data. This map shows a 5-year (2010–2014) composite of landings in kilograms per 2×2 minute lat.×long. grid (Butler and Coffen-Smout, 2017). As a measure of historical adult abundance, we used historical fishery landings data gathered by McCracken (1958). He gathered information on landings from several governing agencies and was able to find sufficient location data to identify important areas (fishing grounds) in the Northwest Atlantic, and he expressed the landings as the annual percentage of shares of halibut landings per NAFO division. These historical landings (1953–1954) predate the intensive Atlantic cod (*Gadus morhua*) trawl fishery of the 1970s and 1980s (Myers et al., 1996) and are considered to represent a regulation-free fishery, when fishing crews were free to relocate operations as they pleased, and maximize their catch per unit of effort (Gillis et al., 1993). Because the distribution of fishing vessels typically achieved an ideal free distribution (Gillis et al., 1993), the footprint of the unregulated fisheries is a good representation of historical spatial distribution of adult halibut. Supporting this notion, the abundance-based shares estimated by McCracken using unregulated fisheries data, along with his report of important and stable fishing grounds, were used to allocate fishing shares proportionally among NAFO divisions when the Canadian halibut fishery was first regulated in 1988 (Neilson et al.[5]).

Analysis

All statistical analyses were performed in RStudio, vers. 3.3.2[7] (RStudio, Inc., Boston, MA), and maps were produced in ArcMap, vers. 10.4.1(ESRI, Redlands, CA). We used functions available in the package dismo, vers. 1.1-4, in R, vers. 3.3.2 (R Core Team, 2016) to build 4 models of species distribution with maximum entropy. Each model tested a different combination of parameterization techniques that can help correct various types of sampling bias as outlined by Fourcade et al. 2013 (Table 1). Our models combined data from 18 research surveys (Suppl. Table 1) (online only). Input consisted of the 1980 records of halibut presence, a random subset of 5000 records of absence, and raster

[7] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

layers for 5 environmental variables (covariates). To account for depth-related biases (because the surveys rarely exceed 400 m, although we know that adult halibut can inhabit depths of ~1000-m (Miller et al., 1991; Cargnelli et al., 1999), the extent of the output prediction layer was limited to the area of the strata sampled. Because of this restriction, it is highly likely that some potentially suitable areas were not mapped; however we contend that we are capturing the majority of juvenile habitat because there is an association between depth and halibut size (Bigelow and Schroeder, 1953; Collette and Klein-MacPhee, 2002) because juveniles typically occupy shallower depths and move deeper with age (e.g., Sigourney et al., 2006).

Our model with the strongest diagnostics incorporated a restricted background (with true absence points) and its data were divided by survey (Table 1). By default, a model will select a set of random "background" locations (in unsampled locations) to represent pseudo-absence points. By using true absence points in place of the background data, valuable information is incorporated into the model. We ran 3 separate models for separate surveys: NS and U.S., GSL, and NF, and then combined the 3 output layers, keeping the largest habitat suitability value for each location. This modeling approach made full use of the data available, and running separate models accounted for inherent differences among the surveys (sampling effort, catchability of gear type, and seasonality (Suppl. Tables 1 and 2) (online only) and enabled a consideration of smaller scale trends and potential spatial variation in habitat preferences in different regions.

To evaluate the models, we performed a cross-validation and compared "area under omission curve" (AUC) values. For cross-validation, we withheld 20% of the input data (test data) when running the model, and then compared corresponding predicted values from the resulting habitat-suitability layer with the true values at the test-data locations (a good model can accurately predict the likelihood of species presence in test-data locations). Cross-validation also produces AUC values that indicate the proficiency of a model in differentiating between presence and absence sites and is the standard for maximum entropy assessment (Elith et al., 2006; Phillips and Dudik, 2008). On a scale from 0 to 1, an AUC value greater than 0.9 is widely accepted as "excellent" or "high" accuracy, and less than 0.6 is generally considered a "fail" because 0.5 means probabilities are no better than random (Phillips and Dudik, 2008; Halvorsen, 2013). For the remainder of the analysis, we used the habitat-suitability layer from the strongest performing model, and we also excluded the GSL because tagging evidence supports the management of this area as that of a separate stock (McCracken, 1958; Neilson et al.[5]; Stobo et al., 1988; den Heyer et al., 2012; Le Bris et al., 2017).

For regional comparisons, we partitioned the habitat-suitability layer using the NAFO and EEZ shapefiles as boundaries and calculated statistics within each division. We quantified suitable habitat by using a classification rule: a pixel was classified as "suitable" if its predicted habitat-suitability value was greater than 0.54. Typically values greater than 0.5 are accepted as the probability of presence of halibut at sites where environmental conditions are 'typical' of presence (Phillips and Dudik, 2008; Elith et al., 2011), and by increasing this threshold, we increased this likelihood. The proportion of the total available suitable habitat to fall within each NAFO division ($\hat{p}_i$) and the catch shares per NAFO division allocated on the basis of abundance of Atlantic halibut ($\hat{p}_i$) were both calculated as

$$\hat{p}_i = \frac{s_i}{\sum_{i=1}^{j} s_i},$$

where the summed suitable habitat (km^2) or the summed survey locations with species presence within i NAFO division (s_i), were divided by the totals summed across all j NAFO divisions. We will refer to these values as "SH-based shares" and "abundance-based shares," respectively.

Assuming a constant relationship between potential abundance and availability of suitable habitat, we plotted the relationship between SH-based shares and abundance-based shares (survey data) against a 1:1 baseline. We interpreted this baseline as "expected habitat productivity" where proximity to the baseline indicates whether the productivity of an area is above, meeting, or below expectations. The abundances determined from research surveys were derived from the same data set used to quantify juvenile habitat. Any positive relationship between habitat and abundance determined from research surveys would suggest that the amount of habitat is related to juvenile production. To explore the empirical relationships between suitable habitat availability and fishery productivity (e.g., Brosse et al., 1999; Holbrook et al., 2000; VanDerWal et al., 2009) we plotted the relationship between SH-based shares and commercial landings in recent and historical fisheries (abundance-based shares [landings]). This approach allowed us to test the feasibility of using the 1:1 baseline and to model suitable habitat shares as a proxy for production and to explore the potential for similarities between adult and juvenile halibut distributions. We further explored this potential overlap in choice habitat by overlaying the habitat-suitability layer with the 2010–2014 Canadian commercial fisheries map of landings, by catch weight (Butler and Coffen-Smout, 2017), and by extracting habitat suitability values associated with recent landings data which have a minimum legal fish size of 81 cm TL (DFO[2]).

There are several assumptions inherent in this approach. First, is that good juvenile habitat leads to high adult abundance. Although we do not have direct evidence to support this assumption, it is supported by the nursery-size hypothesis [stated earlier], and inferred by density-dependent mortality during early life-history stages (Iles and Sinclair, 1982; Rijnsdorp et al., 1992; Gibson, 1994; Beverton, 1995; Sundblad et al.,

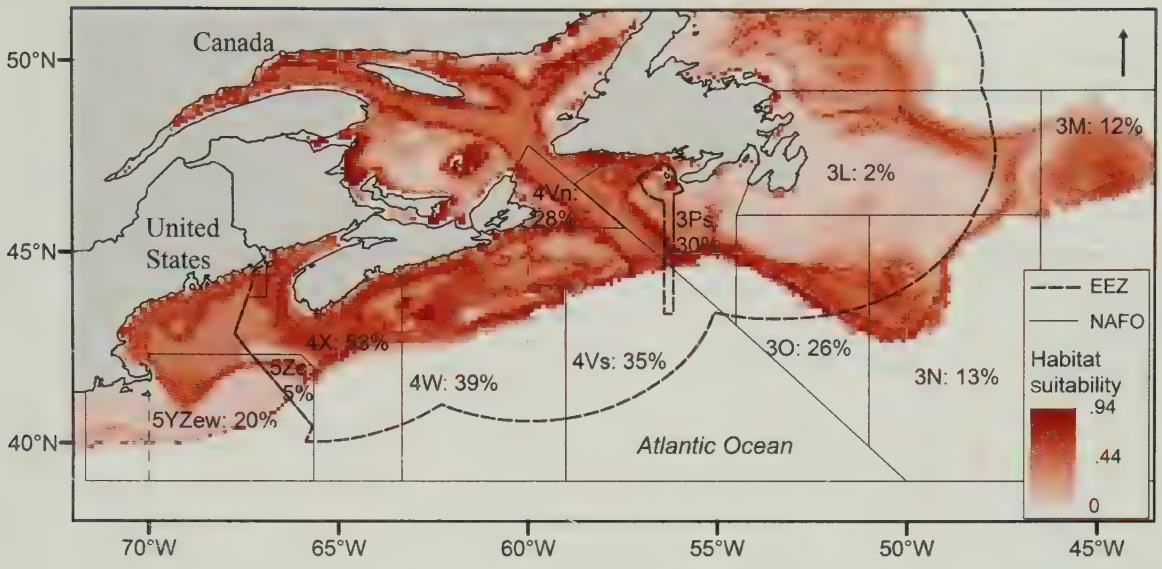

Figure 2

Map of areas in the northwest Atlantic Ocean characterized as suitable habitat for juvenile Atlantic halibut *(Hippoglossus hippoglossus)* and estimated by using maximum entropy species distribution modeling and data from trawl surveys conducted from 2001 to 2013. This habitat suitability layer is a composite output from 3 maximum entropy models for 3 regions in the northwest Atlantic Ocean for which the largest cell value was retained. Habitat suitability is represented on a scale of 0–1, with 0.5 representing the relative habitat suitability and probability of presence of Atlantic halibut where environmental conditions are typical for presence. Percentages represent the total percentage of the area surveyed within each North Atlantic Fisheries Organization (NAFO) division that had suitable habitat. Values for the NAFO divisions in U.S. waters (5Y, 5Zw, and 5Ze) were grouped together.

2014; Wilson et al., 2016). There is also the assumption that there are low levels of emigration from these areas. This assumption is consistent with tagging studies, which have reported that the majority of recaptures occur in the area of initial tagging (McCracken, 1958; Jensen and Wise, 1961; Neilson et al.[5]; Stobo et al., 1988; Kanwit, 2007; den Heyer et al., 2012; Seitz et al., 2016). Finally, the use of landings data as a proxy for abundance has been extensively debated; here we use the spatial distribution of landings as a surrogate for the spatial distribution of the stock (e.g., Pauly et al., 2013).

Results

Model output was a spatial representation of relative habitat suitability for predominantly juvenile Atlantic halibut. Overall, 22.5% of the total surveyed area was characterized as suitable habitat for juvenile halibut (Fig. 2) (we will refer to this as "suitable habitat"). Cross-validation on 20 iterations of the model produced average AUC values of 0.90 for NS and U.S., 0.85 for NF, and 0.92 in the GLS (on a scale from 0 to 1, with 1 being the best possible score) (Suppl. Fig. 1, A–C) (online only). When we compared the habitat suitability values with the test data, locations with presence of Atlantic halibut were far more frequently associated with areas with high habitat-suitability values and absence with low values; this result also promoted confidence in the model (Suppl. Fig. 1, G–I) (online only).

The greatest proportional amount of suitable habitat fell within the divisions 4X and 4W, which are adjacent NAFO divisions that cover a large section of the Scotian Shelf (Table 2; Fig. 2). Divisions 3Ps (off the southern coast of Newfoundland) and 5Y, 5Ze, and 5Zw (Maine) also contained proportionally large amounts of suitable habitat (Table 2; Fig. 2). The majority of the suitable habitat in the United States was concentrated near shore and along Georges Banks, whereas in 3Ps, it was found along the edge of the Laurentian Channel and toward the deeper slopes (Fig. 2). The remaining NAFO divisions had smaller, although noteworthy, amounts of suitable habitat shares (Table 2).

The southern Grand Banks (Newfoundland) fall within NAFO divisions 3L, 3N, and 3O and possess rich fishing grounds, but unlike the Scotian Shelf (where suitable habitat was predicted to be widely available), suitable habitat in this region was located mostly toward the slope (Fig. 2). A noteworthy amount of suitable habitat (18,162 km^2) was outside Canada's EEZ on the southern Grand Banks and the Flemish Cap (Table 3). International waters are sampled less frequently than areas within the EEZ and therefore there is more uncertainty around abundances in these regions.

Variable contributions describe how well a change in a covariate value contributes to changes in habitat

Table 2

The proportional share of suitable habitat for Atlantic halibut (*Hippoglossus hippoglossus*) within each North Atlantic Fisheries Organization (NAFO) division, and as a percentage of total surveyed area within each NAFO division, calculated by using data from trawl surveys conducted from 2001 to 2013 in 3 regions of the northwest Atlantic Ocean: Newfoundland and Labrador (3L, 3M, 3N, 3O, and 3Ps), Nova Scotia and the United States (4Vn, 4Vs, 4W, 4X, 5Y, 5Zc, 5Ze, and 5Zw), and the northern and southern Gulf of St. Lawrence. Habitat suitability for Atlantic halibut was modeled on a scale of 0–1 by using maximum entropy. Proportion of suitable habitat within region (%) represents the availability of suitable habitat at the division level, and SH-based shares represent suitable habitat availability in relation to the entire study area. *In* and *out* refer to inside and outside Canada's Exclusive Economic Zone, and sampling intensity, by division, is given in the number of sampling sets per square kilometer. For locations of NAFO divisions, see the map in Figure 1.

NAFO division	Sampling intensity (sets/km^2)	SH-based shares (%)	Proportion of suitable habitat within region (%)
3L (in)	0.023	2.2	1.6
3L(out)	0.026	0.0	0.0
3M (cap)	0.002	12.3	4.1
3N (in)	0.022	6.7	1.2
3N (out)	0.033	20.0	3.9
3O (in)	0.027	24.0	8.3
3O (out)	0.054	44.3	1.3
3Ps	0.030	29.6	12.1
4Vn	0.012	28.2	3.9
4Vs	0.024	35.4	8.1
4W	0.020	38.8	16.5
4X	0.020	53.4	23.1
5Zc	0.103	4.7	0.3
5Y, 5Ze, 5Zw	0.031	19.7%	15.6%

Table 3

Habitat suitability for Atlantic halibut (*Hippoglossus hippoglossus*) modeled on a scale of 0–1 by using maximum entropy and data from trawl surveys conducted during 2001–2013 in the northwest Atlantic Ocean. To identify suitable habitat in international waters, for North Atlantic Fisheries Organization (NAFO) divisions that comprise both international and Canadian waters, habitat suitability was modeled both as a percentage within (%In) and outside (%Out) Canada's Exclusive Economic Zone (EEZ). Suitable-habitat availability within and outside of the EEZ was estimated as a percentage of the total surveyed area. NA represents areas that (on the basis of model output) contained no suitable habitat.

NAFO division	Area	Area surveyed (km^2)	%In	%Out	No. of samples
3L	Northern Grand Banks	171,489	1.6%	0%	3879
3M	Flemish Cap	64,612	NA	4.1%	108
3N	Southern Grand Banks	74,153	1.2%	3.9%	1922
3O	Southern Grand Banks	43,400	8.3%	1.3%	2052

suitability, and in turn, how closely each variable is related to productivity. All of our modeled variables contributed to the prediction in all 3 subset regions (Suppl. Fig. 1, D–F) (online only). Percent rise and seasonal range in bottom temperature consistently made relatively small contributions, whereas the contribution of seasonal bottom temperatures and depth varied by region (Suppl. Fig. 1, D–F) (online only). NS and U.S., and the GSL had more limited depth profiles, and the majority (80%) of the fish occurred in less than 190 m and 290 m, respectively (Table 4). In contrast, a much broader depth profile was portrayed in NF, where the majority of the catch was below 560 m (Table 4, Suppl. Fig. 2) (online only). Owing to

Table 4

Depth, slope, and bottom temperature (summer, winter, and range) were used as predictor variables to model the distribution and availability of suitable habitat for Atlantic halibut (*Hippoglossus hippoglossus*) by using data from trawl surveys conducted from 2001 to 2013 in the northwest Atlantic Ocean. Empirical cumulative distributions (ECDs), which describe the odds that a positive survey set occurred (Atlantic halibut were present) across the available range of environmental conditions, for each predictor variable, were calculated for 3 regions in the northwest Atlantic Ocean: Nova Scotia and U.S. waters (NS and U.S.), Newfoundland and Labrador (NF), and the northern and southern Gulf of St. Lawrence (GSL). Values in the 10% and 90% columns provide the range for the majority (middle 80%) of the positive sets in each region, and the *D* statistics from Kolmogorov–Smirnov (K–S) tests are all close to 0, supporting the notion that there is no statistically significant difference between environmental conditions at the locations of positive sample data sets and the entire data set and that both data sets are drawn from the same range of variables. B. temp=bottom temperature.

		ECD		K–S test	
Region	Variable	10%	90%	*D* statistic	*P*-value
NS and U.S.	Depth (m)	−193.4	−65.0	0.0026	1
NF	Depth (m)	−556.1	−88.7	0.0010	1
GSL	Depth (m)	−281.0	−30.2	0.0022	1
NS and U.S.	Slope (% rise)	0.0	1.5	0.0000	1
NF	Slope (% rise)	0.1	4.6	0.0000	1
GSL	Slope (% rise)	0.1	1.5	0.0000	1
NS and U.S.	Summer b. temp. (°C)	4.2	8.7	0.0002	1
NF	Summer b. temp. (°C)	2.9	6.7	0.0001	1
GSL	Summer b. temp. (°C)	1.5	5.8	0.0004	1
NS and U.S.	Winter b. temp. (°C)	3.7	7.7	0.0002	1
NF	Winter b. temp. (°C)	2.6	5.4	0.0001	1
GSL	Winter b. temp. (°C)	−0.2	3.7	0.0004	1
NS and U.S.	B. temp. range (°C)	−0.7	2.1	0.0002	1
NF	B. temp. range (°C)	−0.4	1.4	0.0001	1
GSL	B. temp. range (°C)	−0.1	5.3	0.0004	1

a much wider distribution of sample depths in NF, this analysis could benefit from a higher sampling effort in deeper waters across the range; however, with the highest suitability falling well within the depth range of the survey strata, we do not believe that the depth limitation hindered the prediction of suitable habitat for juveniles. Summer bottom temperature had the highest contribution to the NS and U.S., and NF models, whereas winter bottom temperature contributed the most to the GSL model (Suppl. Fig. 1, D–F) (online only). The majority of fish caught in NS and U.S. were caught between summer temperatures of 4.2°C and 8.7°C; a slightly increased prevalence occurred toward the warmer temperatures (Table 4, Suppl. Fig. 2). In NF there was a similar range with a shift toward colder summer temperatures; the middle 80% of juveniles were found in waters from 2.9°C to 6.7°C (Table 4). Alternatively, in GSL, there was a lean toward cooler summer temperatures, between 1.5°C and 5.8°C (Table 4, Suppl. Fig. 2) (online only). These temperature windows are similar to those from GSL pop-up satellite archival tagging studies from Le Bris et al. (2017) and Murphy et al. (2017). Among regions, the environmental variable windows of occurrence of juveniles overlap with slight variations in temperature and depth at the extremes. Lower and upper values correspond with regional differences in habitat characteristics that are evident when the empirical cumulative distributions of reginal samples are compared (Suppl. Fig. 2) (online only).

SH-based shares were directly related to abundance-based shares (survey data), supporting the idea that the 1:1 line can be considered a baseline for expected productivity from each region (Fig. 3A). In turn, both suitable habitat shares and abundance-based shares (survey data) were related to abundance-based shares (landings) in historical (1953–54) and recent commercial fisheries (2010–14) (Fig. 3, B–D). The recent abundance-based shares (landings: 2010–14) from the halibut fishery were also very similar to abundance-based shares (survey data) from 2010 through 2013 (Fig. 3C), and when plotted against suitable habitat availability, relations fell very close to the 1:1 line of expected productivity (Fig. 3B).

There was a strong spatial overlap between halibut fishery landings and suitable habitat (Fig. 4; Butler and Coffen-Smout, 2017). The highest proportion of the 2010 through 2014 catch occurred in division 4X, which

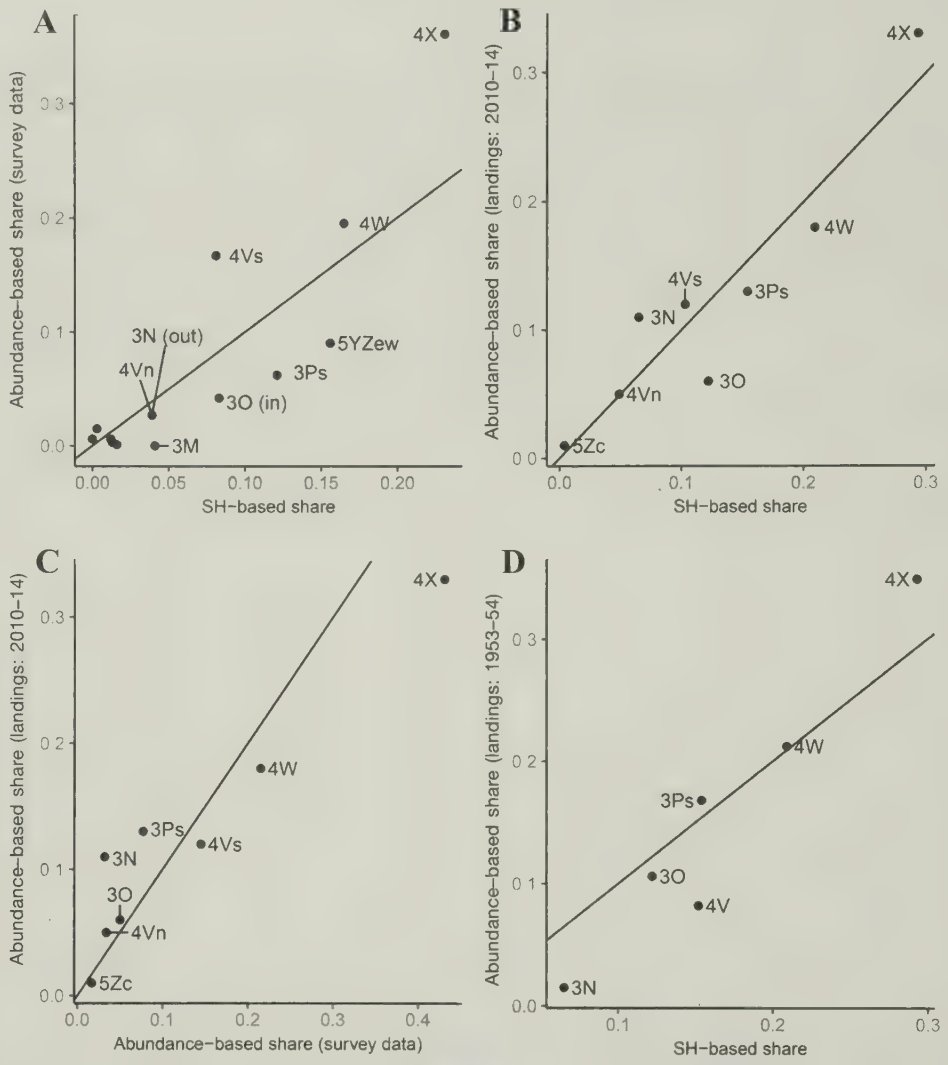

Figure 3

Linear relationships between the availability of suitable habitat and proportional abundances of Atlantic halibut *(Hippoglossus hippoglossus),* by North Atlantic Fisheries Organization (NAFO) division, in relation to the 1:1 line which indicates a baseline for expected productivity for each NAFO division. (**A**) The suitable habitat (SH)-based share (the proportion of the total suitable habitat available within each NAFO division), versus abundance-based share (survey data) (the proportion of the total positive survey sets within each NAFO division), based on data from trawl surveys conducted from 2001 to 2013. Unlabeled points (near the x:y axis) are 3L (out) and 5Zc, clustered above the 1:1 line, and 3L (in), 3N (in), and 3O (out), below the 1:1 line. (**B**) SH-based share versus abundance-based share (landings) (the proportion of the total landings to occur within each NAFO division), based on commercial fishery data for 2010–2014. (**C**) Abundance-based share (survey data) versus abundance-based share (landings), based on commercial fishery data for 2010–2014. (**D**) SH-based share versus abundance-based share (landings), based on commercial fishery data for 1953–1954 (McCracken, 1958).

contained the largest SH-based share (Fig. 4A). The spatial overlap between landings and high suitability values (Fig. 4A) is also supported by the relation between habitat suitability and commercial landings (see histogram [Fig. 4B]), which shows catch frequencies increasing with habitat suitability. To further explore this relationship, we performed a linear regression that predicted landings as a function of suitable habitat availability. The coefficient of multiple determination (R^2) was 0.68, habitat suitability was significant for landings with a level of marginal significance (P) of

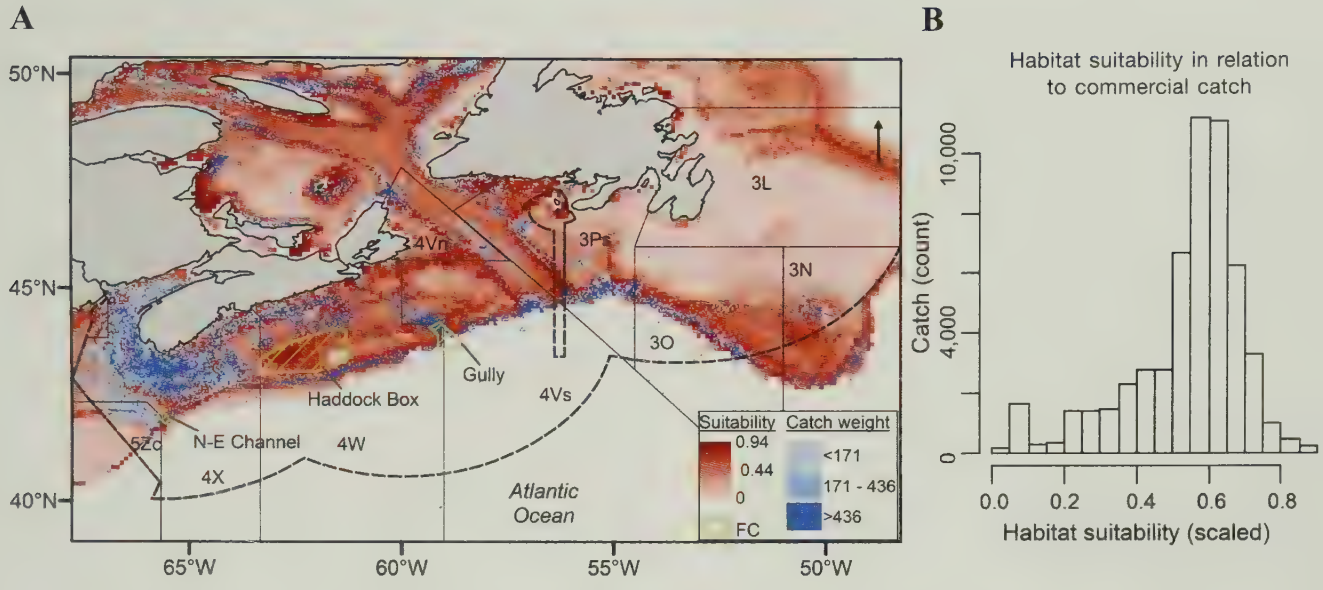

Figure 4

Relationship between commercial landings of adult Atlantic halibut (*Hippoglossus hippoglossus*) during 2010–2014 and suitability of habitat for juvenile Atlantic halibut in the northwest Atlantic Ocean. (**A**) The habitat-suitability layer, developed with data from trawl surveys conducted during 2001–2013, overlaid with the map of catch weight from directed fisheries and bycatch landings from Butler and Coffen-Smout (2017). Fishery closures (FCs) include substantial conservation areas, marine protected areas, and nursery areas where fishing of Atlantic halibut is restricted or not permitted. (**B**) Histogram of habitat suitability versus commercial catch, showing the correspondence between landings and scaled habitat suitability values.

0.0117, and for a few large residuals included in divisions 3O (below) and 4X (above).

Discussion

We provide evidence to support the nursery-size hypothesis, which states that the amount of juvenile habitat available is related to adult production (Iles and Sinclair, 1982; Rijnsdorp et al., 1992; Gibson, 1994; Beverton, 1995; Sundblad et al., 2014; Wilson et al., 2016). We found a direct relationship between juvenile and fishery production within NAFO divisions, and a proportional relationship between suitable-habitat availability, and stock productivity. This is consistent with Wilson et al. (2016), who reported that recruitment among 5 flatfish species is limited by nursery area. They further found that juvenile abundance was related to suitable- habitat availability and, in turn, to the recruitment and abundance of adults. This result is also in agreement with tagging studies which consistently find that most tagged halibut are caught within 200-km or less of the location of release (McCracken, 1958; Jensen and Wise, 1961; Neilson et al.[5]; Stobo et al., 1988; Kanwit, 2007; den Heyer et al., 2012; Seitz et al., 2016), and with more recent research that shows a high connectivity within patches of 227 km^2 (Boudreau et al., 2017)

In this study, NAFO divisions that fall on the 1:1 baseline of the relationship between the SH-based shares and abundance-based shares (survey data) can be considered to be meeting productivity expectations, whereas areas that fall above or below the baseline are exceeding or below expectations, respectively (see Fig. 3). When compared with suitable-habitat availability, juvenile abundance in NAFO divisions 4Vs, 4W, and 4X exceeded expectations, and fell short in NAFO divisions 5Y, 5Ze, 5Zw, 3O, and 3Ps (Fig. 3A). This finding was consistent with previous research that revealed areas with persistently high juvenile halibut abundance within the most productive NAFO divisions (Boudreau et al., 2017). Several factors may be contributing to such trends: variations in current and historic fishing pressures, migrations, prey availability, and environment. Over the past few decades, fishery closures and no-take protected areas, for example, have been established throughout the northwest Atlantic (Butler and Coffen-Smout, 2017). In NAFO divisions 4Vs, 4W, and 4X, the Haddock Box (nursery area), The Gully Marine Protected Area, and the Northeast Channel Coral Conservation Area are substantial areas where trawling and other fishing methods are highly limited or not permitted (Butler and Coffen-Smout, 2017). These areas also have high habitat-suitability values and are located in NAFO divisions where SH-based shares, juvenile abundance, and commercial landings are all high (Fig. 4). Closed areas may also explain why year-round closures on Georges Bank were followed by a dramatic increase in yellowtail flounder populations (Fogarty and Murawski, 2004). Closed areas on the

Scotian Shelf could be benefiting Atlantic halibut and contributing to the stock rebound, both by providing habitat protection and by reducing halibut bycatch in other fisheries.

NAFO divisions 5Y, 5Ze, and 5Zw fell short in juvenile abundance despite adequate suitable habitat availability. Consistent with our findings, Shackell et al. (2016) detected low abundance in relation to suitable-habitat availability in U.S. waters. They, and others, have proposed that this low abundance could be the product of finer-scale stock structure or a history of overfishing (or both) (Seitz et al., 2016; Shackell et al., 2016). Certainly historic fishing pressure is a plausible explanation for the observed low abundances in divisions 5Y, 5Ze, and 5Zw (Grasso, 2008). As biomass decreased during the 1800s in nearshore fishing grounds, exploitation progressed farther offshore and also began to include juvenile populations (Grasso, 2008). The expansion of the fishery extended out from Massachusetts Bay (Fig. 1), which was the first region to see populations decline and which endured the longest period of intense exploitation (Grasso, 2008). This area, once the home of the commercial fishery for Atlantic halibut, has yet to see a rebuilding of halibut stocks (Hennen[4]). The general consensus is that halibut were repeatedly depleted in the United States and more recently depleted throughout their range in the 1990s (Grasso, 2008; Trzcinski and Bowen, 2016). The varying rates of putative recovery throughout the range may be a reflection of smaller-scale stock structure within this stock unit. Boudreau et al. (2017) observed the temporal persistence of several core areas of high juvenile halibut abundance alongside the disappearance of others. A noteworthy core area that disappeared in the 1980s was the area along the shelf edge in NAFO divisions 3O and 3Ps (divisions that we identified as underperforming), while persistent core areas in NAFO divisions 4Vs, 4W, and 4X are associated with our highest performing divisions. Boudreau et al.'s (2017) research supports the Shackell et al. (2016) hypothesis that subpopulations may exist within this Atlantic halibut stock. The erosion of subpopulations could explain why some divisions in our analysis fell below the 1:1 line of expected habitat productivity.

Knutsen et al. (2007) observed genetic subpopulation structure among Greenland halibut (*Reinhardtius hippoglossoides*) and that differentiation increased with distance. They theorized that 2 genetically different populations exist and that ocean currents play a major role in determining population structure (during larval stages). Notably, for this species, dissimilarity between management units and stock structure was identified by genetic analysis (Knutsen et al., 2007). If subpopulations exist, assessing distinct stocks as a single large stock often runs the risk of overestimating stock size; such a practice was likely responsible for the collapse of the stock of Atlantic cod (*Gadus morhua*) (e.g., Sterner, 2007). True spatial overlap between management units and actual underlying population structures supports accurate stock assessments, and therefore a mismatch between the two is reason to revisit respective management regimes (Lundy et al., 1999; Reiss et al., 2009). Here we do not show that subpopulation structures exist within the Scotian Shelf and Southern Grand Banks of Newfoundland Atlantic halibut management unit, but provide reasons to further investigate this possibility.

It is also possible that deviation from the relationship of juvenile:adult abundance (Fig. 3C) may be influenced by ontogenetic shifts in habitat and density-dependent migration. The mechanisms that influence Atlantic halibut movements are not fully understood, but in areas that have reached carrying capacity, it is more likely that animals will emigrate (Fretwell and Lucas 1970; MacCall, 1990). Here, we show a strong positive relationship between habitat suitable for juveniles and commercial landings, and an overlapping distribution of commercial landings and juvenile habitat. This finding is consistent with those from tagging studies that have repeatedly shown that the majority of halibut recaptures are in the area of initial tagging, despite the occasional far-distance movement by an individual (McCracken, 1958; Jensen and Wise, 1961; Neilson et al.[5]; Stobo et al., 1988; Kanwit, 2007; den Heyer et al., 2012; Seitz et al., 2016).

Several next steps can be taken to build on this research and further develop an understanding of Atlantic halibut distribution in the Northwest Atlantic. We limited our model to 5 predictor variables; however additional environmental and community variables, including fishing effort, methods and regulations, prey availability, predation, and interspecific competition, could influence (and potentially improve) the predictive ability of the model. Additionally, by changing existing values of environmental variables (such as temperature or depth), the same model could be used to explore potential changes in suitable-habitat distributions in response to climate change: a valuable resource for planning adaptive measures for a fishery. Overall, our analysis supports the pursuit of future research on potential subpopulation structures and the impact of closed areas on productivity.

Our analysis builds on current ecological knowledge of Atlantic halibut, and can be considered a contribution for future international discussions and assessments of the stock. Our study has shown that suitable habitat can be used as a proxy for juvenile and adult halibut abundance, and that there are areas where population size is below its potential. The Canadian stocks are currently assessed as healthy, and rebuilding is not part of the management objective. However, the occurrence of regions in U.S. waters where abundances remain below expectations indicates that there is room for population growth, which could potentially be achieved through spatial management, more specifically, by the protection of core juvenile habitat. The presence of noteworthy suitable-habitat availability outside the EEZ, off the Grand Banks of Newfoundland also highlights a need for international collaboration. These regions are not regularly surveyed and are sub-

ject to international fishing pressures, making them vulnerable to overexploitation. Our maps of suitable habitat can be used by management in the development of user rights in territorial waters and the establishment of catch limits or no-take areas. For now, we provide a significant step forward in the characterization of spatial patterns of Atlantic halibut productivity in the Northwest Atlantic, and a contribution to future international discussions and management of the growing fishery for this species.

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A comparison of laboratory-holding and tag-return methods for evaluating delayed mortality of Dungeness crab (*Cancer magister*) discarded in Oregon fisheries

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Abstract—The delayed mortality rate of crab discarded during fishing operations can be under- or overestimated in laboratory holding experiments, given the unnatural conditions and the short-term duration of these experiments. To evaluate the extent to which a method affects accuracy in these estimations, we compared mortality rates established through laboratory holding with mortality inferred from a year-and-a-half long tag-return study of Dungeness crab (*Cancer magister*) discarded in Oregon crab fisheries. The reflex action mortality predictor (RAMP) approach, which relates reflex impairment to probability of mortality, was applied in both studies. Similar patterns in mortality- and tag return- rates with respect to fishery, sex, reflex impairment, shell hardness, and injury from the 2 studies lends support to the reliability of the laboratory-generated mortality rates. However, results suggest that mortality rates determined in captivity are likely underestimated when crab are dropped a distance of greater than 6 m (and potentially less) back to water. This underscores the importance of determining the contribution to mortality of variables in the capture, handling, and discard process that are not incorporated in a study to estimate mortality of discarded animals. Both studies also highlighted the significance of sample size when applying the RAMP approach to a fishery with low rates of discard mortality.

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Mortality can result from the fishing, handling, and discard process for nontarget animals, either immediately after capture or after a delay (Benaka et al., 2014). To evaluate the mortality of discarded animals (henceforth termed "delayed discard mortality"), a variety of methods have been employed. These include the following: 1) captive-holding methods (Kennelly et al., 1990; Bergmann et al., 2001; Parker et al., 2003); 2) mark-recapture methods (Kruse et al., 1994; Watson and Pengilly[1]; Trumble et al., 2000); and 3) results from telemetric studies, including that use radio- (Raby et al., 2012; Nguyen et al., 2014), acoustic- (Pepperell and Davis, 1999; Donaldson et al., 2012; Yergey et al., 2012), and satellite-tracking tags (Gallagher et al., 2014). Also used are 4) in situ net pens or cages (Diamond and Campbell, 2009; Brownscombe et al., 2015; Bower et al., 2016); and 5) in situ visual monitoring (Campbell et al., 2010; Hochhalter, 2012; Brownscombe et al., 2014; Danylchuk et al., 2014).

In conjunction with methods to determine mortality, the reflex action

[1]Watson, L. J., and D. Pengilly. 1994. Effects of release method on recovery rates of tagged red king crabs *Paralithodes camtschaticus* in the 1993 Bristol Bay commercial fishery. Reg. Inf. Rep. 4K94-40, 21 p. Alaska Dep. Fish Game, Kodiak, AK.

mortality predictor (RAMP) approach has been developed (Davis and Ottmar, 2006). This method relates impairment in reflex actions to the probability of mortality. This relationship is established by first selecting reflexes that give a consistent, instantaneous, and involuntary response to a stimulus. After enduring the set of stressors associated with fishing and discarding (either directly during fishing operations or through simulation in a laboratory), the animals can be evaluated by determining whether each of these reflexes is present. To relate the levels of reflex impairment (i.e., the total number of missing reflexes) to the probability of mortality, survival must be determined by using one of the methods described previously (captive holding, tagging, etc.). A "RAMP relationship" is subsequently created by determining the number of animals, for each level of impairment, that die out of those monitored for mortality. Once established, this relationship can be applied to reflex-impairment data collected over the spatial and temporal extent of a fishery, making the mortality rates more representative of the fishery at large.

The efficacy of a RAMP relationship is linked with the reliability of the predicted delayed mortality rates. Therefore, it is essential to consider method-specific biases and limitations. For example, it is important to evaluate the contribution to mortality from tagging for identification (Tegelberg and Magoon, 1971; Wassenberg and Hill, 1993) or telemetry studies, or the contribution that is due to the effect of captivity in research that determines mortality through holding animals (Yochum et al., 2015; Yochum et al., 2017). In addition, methods that do not allow long-term monitoring may underestimate mortality rates caused by chronic, enduring impairment (Wassenberg and Hill, 1993; Bergmann and Moore, 2001).

Mortality rates estimated through captive holding are biased by the unnatural environment or holding conditions (or both) (Yochum et al., 2015; Yochum et al., 2017). Mortality rates could be overestimated because of agonistic interactions or predation among captive animals, suboptimal temperature or water quality, density of animals in holding enclosures, or failure to meet other biological or environmental requirements of the captive animal (Simonson and Hochberg, 1986; Kondzela and Shirley, 1993; Wassenberg and Hill, 1993; Spanoghe and Bourne, 1997; Portz et al., 2006; Weltersbach and Strehlow, 2013). Alternatively, mortality rates could be underestimated because mortality resulting from an animal's inability to obtain food or avoid predation is not incorporated in such studies (Durkin et al., 1984; Uhlmann et al., 2009; Benoît et al., 2010; Urban, 2015). Similarly, the effect of displacement from suitable habitat and the impact from the return to water after capture and handling onboard are not often considered.

Despite limitations of captive holding, RAMP relationships have commonly been created by using onboard holding tanks or laboratory-based holding facilities (Davis, 2007; Stoner et al., 2008; Humborstad et al., 2009; Barkley and Cadrin, 2012; Stoner, 2012; Hammond et al., 2013; Rose et al., 2013; Depestele et al.[2]; McArley and Herbert, 2014; Humborstad et al., 2016). Preference for this approach is largely due to advantages over alternative methods, which include providing scientists with control and allowing them to differentiate causes of mortality, observing degradation in health and changes in behavior, and knowing the time of death (Davis and Ryer[3]). Because short-term laboratory holding is frequently used to estimate delayed discard mortality rates, we conducted a field validation study to assess the limitations of this approach. This was done by comparing results from 2 RAMP studies that evaluated delayed mortality, one through tag-returns and one by using laboratory holding. The former study and comparison are described here, and the latter was reported by Yochum et al. (2017). Tagging was selected for the comparison because it allows an evaluation of long-term mortality rates and allows animals to experience more natural conditions after release.

The Oregon (U.S.A.) commercial and recreational Dungeness crab (*Cancer magister*) fisheries were selected for this study because of their high level of discard, and because Oregon fishermen have experience with tagging studies for these crab, which yielded high tag-return rates (Jow, 1965; Snow and Wagner[4]; Demory[5]; Hildenbrand et al.[6]). Additional factors that make Dungeness crab a good candidate for comparing discard mortality in situ and in the laboratory include evidence that they 1) are agonistic and cannibalistic (Jacoby, 1983; Fernández, 1999; Barber and Cobb, 2007), 2) are often preyed upon by seabirds and California sea lions (*Zalophus californianus*) upon their return to the water, and 3) like many crustaceans, can be difficult to maintain in captivity owing to stress, disease, and sensitivity to temperature and water quality (Burton, 2001; Barrento et al., 2008).

In Oregon, only male Dungeness crab at or above 159 mm (6.25 in) carapace width (measuring the straight line distance across the carapace, shell edge to shell

[2] Depestele, J., E. Buyvoets, P. Calebout, M. Desender, J Goossens, E. Lagast, D. Vuylsteke, and C. Vanden Berghe. 2014. Calibration tests for identifying reflex action mortality predictor reflexes for sole (*Solea solea*) and plaice (*Pleuronectes platessa*): preliminary results. ILVO-commun. Rep. 158, 30 p. [Available from website.]

[3] Davis, M. W., and C. H. Ryer. 2003. Understanding fish bycatch discard and escapee mortality. AFSC Q. Rep. 2003, Jan–Mar, 9 p. Alaska Fisheries Science Center, Seattle, WA. [Available from website.]

[4] Snow, C. D., and E. J. Wagner. 1965. Tagging of Dungeness crabs with spaghetti and dart tags. Fish Comm. Oregon, Res. Briefs 11:5–13.

[5] Demory, D. 1971. Crab movement off Port Orford, Oregon. Shellfish Invest. Inf. Rep. 70-7. Res. Div., Fish Comm. Oregon, Salem, OR.

[6] Hildenbrand, K., A. Gladics, and B. Eder. 2011. Crab tagging study: adult male Dungeness crab (*Metacarcinus magister*) movements near Reedsport, Oregon from a fisheries collaborative mark-recapture study, 21 p. Oregon Wave Energy Trust, Portland, OR.

Table 1

Reflexes used to assess vitality of Dungeness crab (*Cancer magister*) when applying the reflex action mortality predictor approach for predicting discard mortality, as detailed in Yochum et al. (2017), along with the method for assessment and metrics for determining whether a given reflex is present (a state that includes weak responses) or absent. Reflexes were assessed in the order (1–6) shown.

Order	Reflex	Method	Present	Absent
1	Eye retraction	A probe is used to lightly tap the top of an eye	Crab retracts the eye downward	Crab does not react, leaving the eye in place
2	Mouth defense	A probe is used to attempt to pull the 3rd maxillipeds forward	Crab defends its mouthparts with its chela making it difficult to access the maxillipeds	Crab allows its maxillipeds to be manipulated
3	Chela closure	A probe is placed below the chela dactyl	Crab reacts by closing the chela tightly, then opening it again without manipulation	Crab does not open and close its chela without manipulation
4	Leg wrap	A probe is used to pull pereopods 2–4 to a 180° angle	Crab draws the pereopods back in (i.e., joints at less than a 180° angle)	Crab pereopods do not move without manipulation
5	Leg curl	Pereopod 5 is straightened and pulled downward	Crab pulls up and curls its pereopod in a controlled manner	Crab does not move the pereopod without manipulation
6	Abdomen response	A probe is used to attempt to pull the top of the abdominal flap away from the crab's body	Crab exhibits a strong, agitated reaction	Crab does not react

edge, anterior to the tenth anterolateral spine, not including the spines) may be retained in the commercial fishery, and at or above 146 mm (5.75 in) in the recreational fishery. Legal-size, soft-shell males are also typically discarded to allow them to harden and fill with flesh after molting (PSMFC[7]; ODFW[8]). Through logistic regression modeling, Yochum et al. (2017) estimated delayed discard mortality rates (i.e., the proportion of discarded animals that die within 5 d of release) for the commercial ocean fishery and recreational bay fisheries (both from a boat and shoreside, i.e., fishing from land rather than a boat, often from a dock or pier). The goal of the tagging study described here was to ascertain whether 1) the laboratory study reported by Yochum et al. (2017) under- or over-estimated the true mortality rates for discarded Dungeness crab, 2) whether there are long-term, chronic effects (attributed to persistent impairment) that lead to delayed mortality that were obfuscated by using short-term monitoring, and 3) whether the impact from the return to water during the process of discarding, a stressor not incorporated in the laboratory study, contributes to mortality. Crab are susceptible to cracked carapaces or fatal injuries (or both) when being dropped from a vessel, dock, or pier. Mortality attributed to this impact could therefore explain differences in rates estimated between laboratory and tagging studies and would suggest the importance of including this variable in an estimation of mortality to improve accuracy. Through this research, we also aimed 4) to evaluate tag-return methods for estimating mortality rates based on RAMP scores.

Materials and methods

Laboratory-holding study

For the laboratory-holding study (see Yochum et al., 2017 for details), between February 2012 and April 2014, crab intended for discard were assessed during 22 commercial fishing trips by an accompanying scientist ("ride-alongs") along the Oregon coast. During the same period, an additional 26 recreational fishing trips were completed on a boat in Yaquina Bay (in Oregon), and sampling of the recreational shoreside fishery was completed on 15 occasions at the Port of Newport Public Fishing Pier (Yaquina Bay). A systematic random sample of crab from the commercial fishery, and all "recreationally" caught crab were assessed when they would have been released (i.e., after all handling processes), typically within 10 min of being landed (usually sooner). Crab assessments (completed in less than 1 min per crab) included the following variables: sex,

[7] PSMFC (Pacific States Marine Fisheries Commission). 1978. Dungeness crab project of the state-federal fisheries management program, 139 p. Pac. States Mar. Fish. Comm., Portland, OR.

[8] ODFW (Oregon Department of Fish and Wildlife). 2015. 2015 Oregon sport fishing regulations, 100 p. Oregon Dep. Fish Wildl., Salem, OR.

Figure 1

Photograph of a Dungeness crab (*Cancer magister*) tagged with a double t-bar anchor tag (TBA-LEVO) for this study in which Dungeness crabs were tagged and released between October 2012 and April 2014 off the coast of Oregon and in Yaquina Bay, Oregon

shell hardness ("soft": little or no hardening after molting; or "hard": nearly fully hard to near molt), carapace width, presence of new injuries, and amount of time spent out of water before assessment. In addition, each crab was evaluated for presence or absence of the 6 RAMP reflexes established for assessing Dungeness crab vitality (Table 1) and was given a reflex impairment score ("score") equal to the number of absent reflexes (0–6; both weak and strong reflex responses were considered present reflexes). During sampling, 12% of crab intended for discard (n=1065), representing all impairment scores, were transported to a laboratory for holding to determine mortality rates. Owing to an observed captivity effect for crab of all scores (including score-0 crab), a crab was considered a "mortality" only if it died within the first 5 d of holding.

Tag-return study

During the aforementioned sampling trips, beginning in October 2012, we aimed to tag and release all crab not intended for laboratory holding that were also not too small or soft to tag. Crab were tagged with a lime green double 't-bar' anchor tag (TBA-LEVO, Hallprint Fish Tags,[9]Hindmarsh Valley, Australia; Fig. 1), the same tag type that was used for identification purposes in the laboratory holding study. Details of tag selection and tagging procedure are provided in Yochum (2016). Tagged crab were released at location of capture, in a manner that attempted to mimic the discard process of a fisherman. Care was taken to randomize and balance the number of crab that were tagged and released vs. returned to the laboratory, over different combinations of score, sex, and shell hardness (Table 2). The same data obtained for held crab were collected for those tagged and released.

An extensive outreach campaign began before the commencement of the tag-return study and was a focal part of the project throughout its duration. To encourage the participation of fishermen (Pollock et al., 2001), for each tag returned (either the physical tag or a picture of the tag was required) fishermen were given $20, a hat or a shirt, and an entry ticket for 2 cash-prize raffles that took place in October 2013 and August 2014. Outreach efforts to make fishermen aware of the rewards and project included the following: frequently talking with fishermen (captains and crew) at the docks (and elsewhere) and inquiring if they had tags to return, regularly posting flyers at local docks and in fishing and marine supply stores, and taking additional measures detailed in Yochum (2016). Oregon Sea Grant provided the location where fishermen could return tags and collect rewards in person. We hoped that this arrangement would encourage tag returns given that this organization and location are well known and frequented by fishermen, and because

[9] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

Table 2

Total number of Dungeness crab (*Cancer magister*) that were tagged and released between October 2012 and April 2014 and whose tags were returned, by fishery (commercial ocean off Oregon and recreational in Yaquina Bay, Oregon, by boat and shoreside). Totals are given by sex and shell hardness (combined), and reflex impairment score, which is equal to the number of absent reflexes (out of 6 reflexes assessed).

		Reflex impairment score							
		0	1	2	3	4	5	6	Total
Commercial									
Total	Tagged	2432	334	85	20	5	2	6	2884
	Returned	242	32	4	0	0	0	0	278
Female hard-shell	Tagged	1429	226	70	20	5	2	6	1758
	Returned	86	12	3	0	0	0	0	101
Female soft-shell	Tagged	37	5	1	–	–	–	–	43
	Returned	1	0	0	–	–	–	–	1
Male hard-shell	Tagged	871	97	12	–	–	–	–	980
	Returned	148	20	1	–	–	–	–	169
Male soft-shell	Tagged	95	6	2	–	–	–	–	103
	Returned	7	0	0	–	–	–	–	7
Recreational-boat									
Total	Tagged	831	57	19	2	1	0	1	911
	Returned	108	11	2	1	0	0	0	122
Female hard-shell	Tagged	114	9	–	–	–	–	1	124
	Returned	6	1	–	–	–	–	0	7
Female soft-shell	Tagged	35	2	1	–	–	–	–	38
	Returned	2	0	0	–	–	–	–	2
Male hard-shell	Tagged	586	38	17	1	1	–	–	643
	Returned	87	7	1	1	0	–	–	96
Male soft-shell	Tagged	96	8	1	1	–	–	–	106
	Returned	13	3	1	0	–	–	–	17
Recreational-shoreside									
Total	Tagged	266	22	7	3	0	0	0	298
	Returned	29	1	0	0	0	0	0	30
Female hard-shell	Tagged	46	–	1	1	–	–	–	48
	Returned	4	–	0	0	–	–	–	4
Female soft-shell	Tagged	14	–	–	–	–	–	–	14
	Returned	0	–	–	–	–	–	–	0
Male hard-shell	Tagged	184	20	4	1	–	–	–	209
	Returned	23	1	0	0	–	–	–	24
Male soft-shell	Tagged	22	2	2	1	–	–	–	27
	Returned	2	0	0	0	–	–	–	2
Total	Tagged	3529	413	111	25	6	2	7	4093
	Returned	379	44	6	1	0	0	0	430

this was the place where fishermen returned tags for a previous Dungeness crab tagging study. We attempted to make the tag return process simple by providing multiple ways to exchange the tag for a reward, by requiring minimal paperwork, by allowing fishermen to be instantly rewarded with cash, and by distributing tag-return packets that included tag-return forms, a pen, tape to attach the tag to the form, information on the project, and where to return tags, all inside a waterproof envelope.

Relative short-term survival

We compared relative short-term (5-d) survival data from the Yochum et al. (2017) laboratory study with data from the tag-return study described here to determine whether delayed mortality rates for discarded Dungeness crab were under- or over-estimated when using laboratory-based RAMP methods. We evaluated relative survival rates between score-0 crab (i.e., no reflex responses missing) and those with scores greater than 0, using an approach described by Hueter et al. (2006). This analysis estimates relative survival between 2 conditions of animals (e.g., good vs. poor) and is done with the assumption that there is a disproportionate survival between the 2 conditions during a short-term "recovery period," and that subsequent survival rates are assumed to be equal for both conditions. The "recovery period" was set at 5 d because the laboratory study considered mortalities only with-

in that time frame because of a captivity effect. For the analysis, "condition 1" was assigned to crab with a reflex impairment score equal to 0. Owing to small sample sizes, scores 1–6 were combined and assigned as "condition 2." Sample size was reduced because of limited numbers of crab with scores greater than 0 for these fisheries and because the comparison had to be done by fishery, sex, and shell hardness given that the laboratory study determined different mortality rates for these variables.

Relative survival rates between conditions 1 (score 0) and 2 (score greater than 0) after the "recovery period" (i.e., 5 d in holding for the laboratory study, and 5 d at large for the tag-return study) were estimated for both studies and compared. This was done with all data combined for the laboratory study, and by release event (i.e., sampling trip) for the tag study to control for the influence on return rate of days-at-large, natural and fishing-induced mortality, and temporal variability in catchability, fishing effort, tag loss, and reporting rate.

$$\widehat{R} = \frac{C_2 / C_1}{T_2 / T_1}, \quad (1)$$

where C_i = Number of 'surviving' crab after the recovery period (tag study: recaptured tags; laboratory study: surviving crab) for the ith condition

T_i = Total number of experimental crab (tag study: tagged; laboratory study: held) for the ith condition.

Two-sided confidence intervals (CIs) for the survival rates were calculated to compare the 2 studies. They were calculated as (Hueter et al., 2006):

$$\left(\widehat{R}e^{-Z_{1-\alpha/2}\sqrt{\upsilon}}, \widehat{R}e^{Z_{1-\alpha/2}\sqrt{\upsilon}}\right), \quad (2)$$

where $Z_{1-\alpha/2}$ is the 100 (1–α/2)th percentile of the standard normal distribution and

$$\upsilon = \frac{T_1 - C_1}{T_1 C_1} + \frac{T_2 - C_2}{T_2 C_2}. \quad (3)$$

Relative long-term survival

If there was a more chronic, sublethal effect from the capture, handling, and discard process (e.g., nonlethal physiological impact or change in behavior), a difference in survival rates between conditions could continue beyond a short recovery period (here, 5 d). This difference in survival would indicate that laboratory holding under-estimates mortality by evaluating only over the short-term. To evaluate the potential change in relative survival, by condition over time, we used logistic regression in R software, vers. 3.1.1 (R Core Team, 2014) to model the probability that a recaptured tag was from a condition 2 (score greater than 0) crab, including a variable for days-at-large, and 3 indicators of sex and shell hardness. This analysis allowed us to determine whether the odds of return between the 2 conditions change over time. A nonzero time-dependent slope coefficient indicates different long-term survival between conditions. The intercept would be 0 if the same number of tagged crabs were released in the 2 conditions and they suffered the same rate of short-term mortality after 5 d at large (t=0). If the 2 conditions had the same short-term survival, a nonzero intercept would reflect the ratio of the number of tagged animals in the 2 conditions at t=0. We compared crab within a release event with the assumption that relative natural mortality, catchability, and reporting probability are the same for a given condition and release event.

Evaluating the return to water

In addition to the laboratory holding and tag-return studies, 2 experiments were conducted, one in November 2013 and a second in April 2014, to evaluate the contribution to discard mortality by dropping crab into water. This is a potential cause of different mortality rates between the tag and laboratory studies, and a possible source of error in laboratory-determined mortality rates. For these drop studies, score-0 crab were collected by using recreational fishing gear, tagged, and were held for 2 weeks before experimentation. Then, for each drop height of each experiment, 20 crab at a time were taken out of holding and, for transport to the drop location, were placed in a large ice chest filled with wet burlap (to provide barriers among the crab). For the second study conducted in April 2014 only, the ice chest used for transport was filled with sea water in addition to the burlap so that the crab were in water until they were dropped. At the drop location (approximately 200 m away), 3 crab at a time were taken out of the ice chest, lifted to one of 3 drop heights, and released (dropped) one-by-one into a tank of sea water. Drop heights for both experiments were 8 m ("high") and 3 m ("medium"). Crab were also dropped from 1 m ("low") for the first study and from 6 m ('high') for the second study. The drop distances reflected an attempt to mimic the distance a crab would typically fall during discard from recreational and commercial vessels ("low" and "medium" distances, respectively). The "high" distances were approximations of the maximum distance that a crab would be thrown from a pier or dock during shoreside recreational fishing at low tide (8 m), and a height similar to the distance from the rail of the Newport Pier to the water at mean lower low water (6 m). For the first experiment, we attempted to drop half of the crab from each height such that they would land dorsally and the other half ventrally. For the second experiment, the side on which the crab landed was not forced (merely noted). After 3 crab were dropped, they were removed from the sea water tank and placed in an ice chest filled with sea water and burlap. For each height treatment, once all 20 crab were dropped, they were taken back to the holding tanks and placed in individual compartments, and mortality was determined after 5 d.

Table 3

Information on Dungeness crab (*Cancer magister*) that were tagged and released between October 2012 and April 2014 and differences between crab that were and were not recaptured and their tags returned (all release events combined) for the commercial ocean fishery off Oregon and recreational fisheries in Yaquina Bay, Oregon, by boat and shoreside. Information includes the number of days at large (time between release and recapture of crab for which tags were returned and between release and end of the study for crab for which tags were not returned), carapace width, reflex impairment score (score), water depth at the location the tagged crab was released, and the number of days from the opening of the fishery in which the tagged crab was released (commercial fishery only).

	Tag returned		Tag not returned	
	Mean	Range	Mean	Range
Commercial				
Days at large	107	2–468	499	209–590
Carapace width (mm)	155	138–171	154	52–193
Score	0.14	0–2	0.25	0–6
Depth at release (m)	49	5–150	51	5–150
Days from opening of fishery	66	0–198	83	0–198
Recreational—boat				
Days at large	78	0–449	448	136–674
Carapace width (mm)	137	104–183	127	82–167
Score	0.15	0–3	0.12	0–6
Depth at release (m)	14	4–28	14	4–28
Recreational—shoreside				
Days at large	79	0–163	268	146–672
Carapace width (mm)	124	106–154	119	86–159
Score	0.03	0–1	0.16	0–3

Logistic regression modeling in R software was used to determine whether there is a relationship between drop height and the probability that a crab died within 5 d of holding, and whether any other variables influenced the likelihood of survival, including 1) the November 2013 vs. April 2014 experiment (the difference between the 2 being whether or not the crab was kept in water before being dropped), 2) the side on which the crab landed (dorsal, ventral, or side), 3) carapace width (in millimeters; continuous), 4) sex, 5) shell hardness (soft or hard), and 6) whether or not the carapace cracked as a result of the drop. Model coefficients were estimated by using maximum likelihood (Ramsey and Schafer, 2002) based on the fate (mortality or survival) of individual crab that were held after the drop experiments. Akaike information criteria were used to determine the most parsimonious model for the data.

Results

Tag-return study

A total of 4093 live crab intended for discard were tagged and released, and 430 tags were returned by 15 August 2014 (11%; Table 2). Tags were returned by 207 different fishermen, ranging from 1 to 60 tags/fisherman (average: 2 tags/fisherman; mode: 1 tag/fisherman). When the date of recapture was known, 3 tagged crab were recaptured the same day on which they were released, 53 within the first week at large (12% of the returns), 142 within the first 30 d (33%), 295 within the first 100 d (69%), and 415 within a year (97%). The longest time between release and return was 468 d (Table 3). On average, returned tags were at large for 98 d. With respect to movement, the Euclidean distance from release to recapture locations ranged from 0 to 150 km (Fig. 2), and there was no relationship between days-at-large and total distance. Some of the farthest distances (>100 km) occurred within a week at large, and some of the shortest distances (<1 km) were detected after a year. The majority (73%) of recaptured crab, however, were caught less than 10 km from the release location (59% for the commercial fishery; 98% and 100% for the recreational by boat and shoreside fisheries, respectively). For the recreational fisheries, 43% (by boat) and 58% (shoreside) of recaptures were within 1 km. For the commercial fishery, 93% of crab were recaptured within 50 km, indicating that the probability of recapture was likely not reduced by animals moving out of the area. There was a pattern that recaptures were closer to shore at the start of the

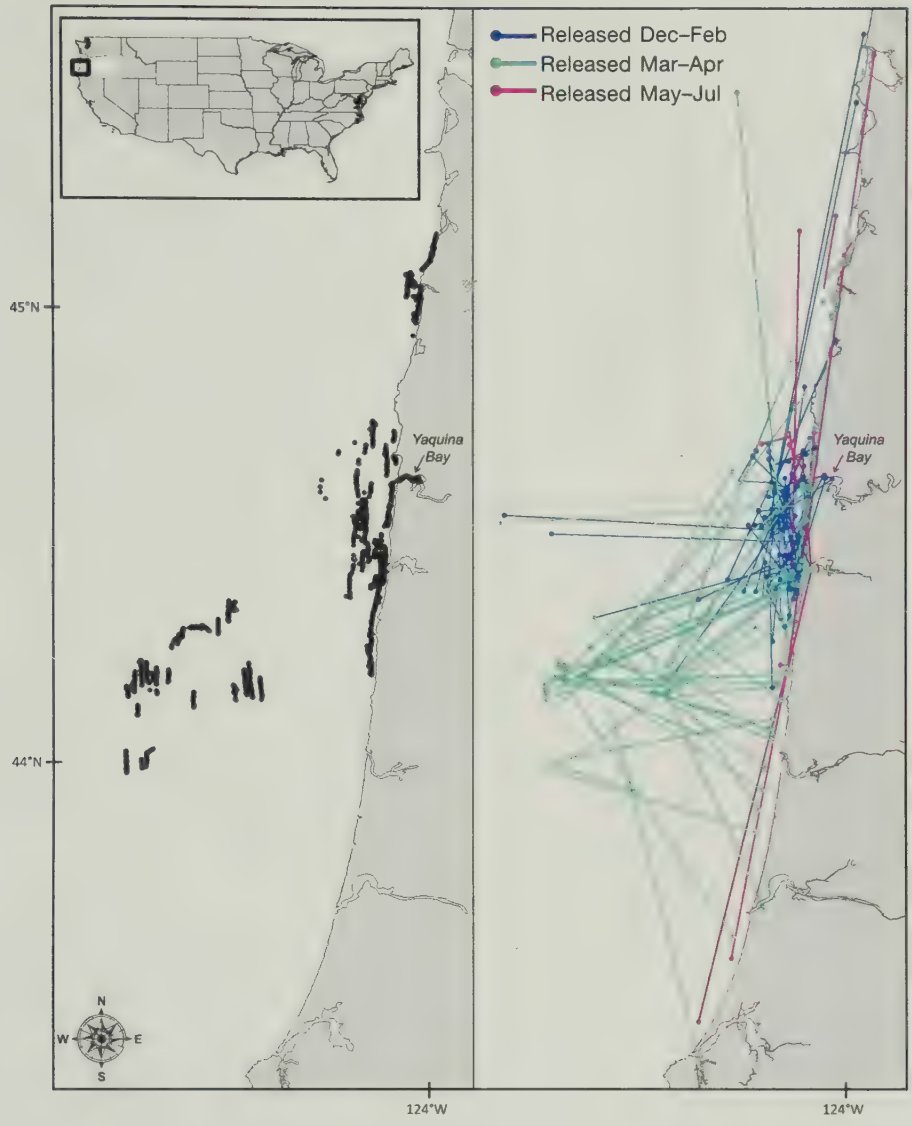

Figure 2

Map showing locations where Dungeness crab (*Cancer magister*) were tagged and released between October 2012 and April 2014 for the commercial ocean fishery and for recreational fisheries (**left panel**) and release and recapture locations of crabs released during ride-along commercial ocean fishing trips only (**right panel**). The dots (right panel) indicate recapture locations and the lines connected to the release location indicate the total Euclidean distance between release and recapture locations.

fishery (December–February; Fig. 2); however, it is difficult to disentangle movement of the crab from that of the fishermen (Demory[5]; Hildenbrand et al.[6]; Barry[10]).

For tag return rates, the highest was for male hard-shell crab (16%, 289 of 1832), followed by male soft-shell crab (11%, 26 of 236), female hard-shell crab (6%, 112 of 1930), and female soft-shell crab (3%, 3 of 95; Table 2; Fig. 3). For score-0 crab only, the proportions of returns did not change from the values listed above, with the exception of returns for male soft-shell crab (10%). For all sex and shell hardness combinations, the average score for noninjured crab was lower than that for injured crab (all combined: 0.18 noninjured; 0.49 for injured). With respect to returns by score, the commercial and shoreside fisheries had decreased returns as score increased, whereas there was no clear pattern for the recreational bay fishery from a boat.

Differences were detected between tagged crab that were and were not recaptured (Table 3). Returned tags were from crab that had lower scores, on average, than

[10]Barry, S. 1983. Coastal Dungeness crab project. Washington Dep. Fish., Proj. Compl. Rep. Project No. 1-135-R, 60 p. Washington Dep. Fish., Olympia, WA.

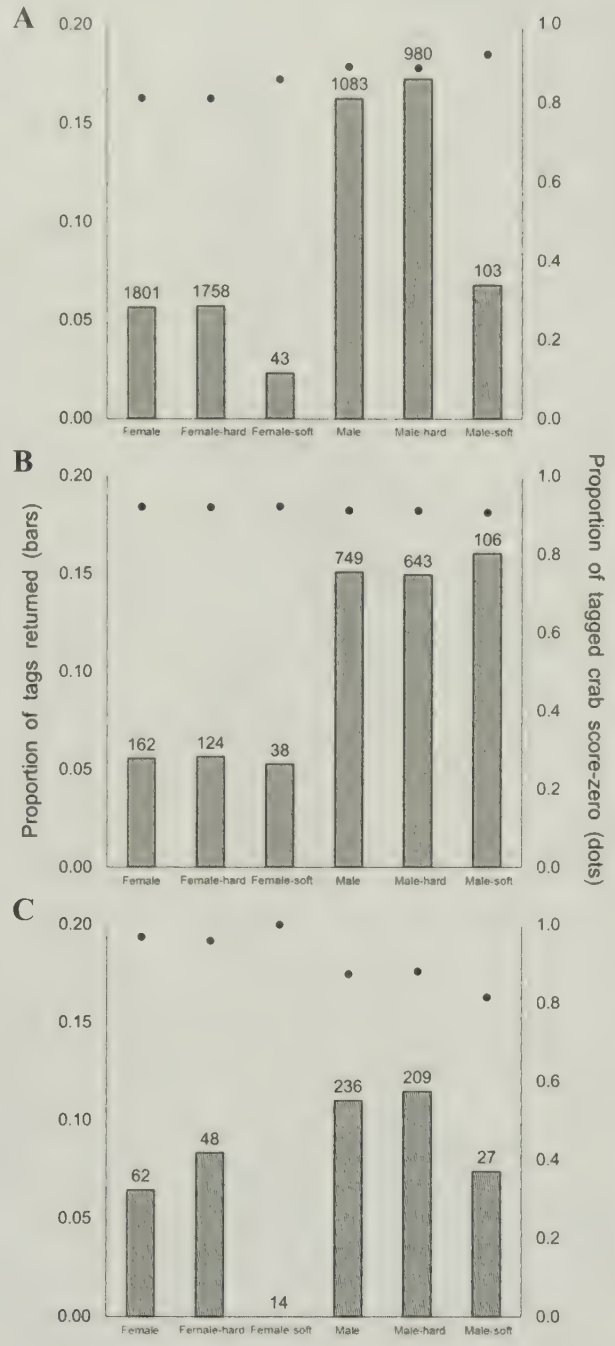

Figure 3

The proportion of Dungeness crab (*Cancer magister*) tagged and released between October 2012 and April 2014 whose tags were returned (vertical bars) and the proportion of tagged crab that were assigned a reflex impairment score of 0 (i.e., no missing reflexes; dots) by fishery for **(A)** the commercial ocean fishery off Oregon and recreational fisheries in Yaquina Bay, Oregon, **(B)** the recreational boat fishery, and **(C)** the shoreside recreational fishery. The reflex impairment score was further differentiated by sex and shell hardness. The numbers above the vertical bars indicate the total number of crabs for each category that were tagged and released.

crab whose tags were not returned. Also, nonreturned tags were on smaller crab, on average, than those returned, and the minimum size was smaller. There was minimal cross-over among the 3 fisheries (Fig. 2). Of tags released in the commercial fishery, 90% were recaptured during commercial fishing operations. For those tagged during recreational fishing by boat, 96% were recaptured by recreational fishing and 3% by commercial fishing. For those released at the Newport Pier, 96% were recaptured by recreational fishing and 4% by another means.

Commercial ocean fishery There were 13 tag and release events for the commercial ocean fishery, and 10% of tags were returned (278 of 2884; Table 2). Males had higher tag return rates than females (16% vs. 6%), and, for both sexes, hard-shell crab had higher return rates than soft-shell (10% vs. 5%; Fig. 3). For female hard- and soft-shell crab, and male hard- and soft-shell crab, the percentages of tags applied to score-0 crab were 81%, 86%, 89%, and 92%, respectively. The proportion of tags returned was highest when released at the start of the fishing season (2011–12 season opened on 15 December; 2012–13 season on 31 December; and 2013–14 season on 16 December), and decreased over the following months toward the end of the season (15 August; Fig. 4). This pattern was observed regardless of the composition of tagged crab, by sex and shell hardness, or the proportion of tagged crab that were score-0. Similarly, an evaluation of the cumulative proportion of tags returned over time, by release event, revealed higher overall return rates when tags were released closer to the beginning of the season, and that days-at-large influenced overall returns less than month of release (Fig. 5).

Recreational fisheries For the recreational bay fisheries by boat and shoreside, there were 19 and 8 release events, respectively (Table 2), and, 13% (122 of 911) and 10% (30 of 298) of tags were returned. For tags recovered by recreational fishing gear, 66% were caught in pots and 25% in rings. For the "by boat" fishery, 3% of injured crab were returned compared with 14% of noninjured crab (all other variables combined). Also, although return rates for this fishery were similar for crab with hard- and soft-shells (15% to 16% for males; 6% and 5% for females), overall return rates for females were lower than for males (Fig. 3). Patterns in tag-return data suggest that the probability of return was not clearly linked with reflex impairment score or shell hardness (Fig. 3), and was lower in general than the other fisheries. Finally, unlike the commercial fishery, there were no clear temporal patterns in returns.

For the "shoreside" fishery, tag-return rates were higher for males than for females (11% vs. 6%; Table 2), and, within sex, for hard-shell crab than for soft-shell crab (8% vs. 0% for females; 11% vs. 7% for males), regardless of the proportion that were score-0 (Fig. 3). Also for this fishery, there were

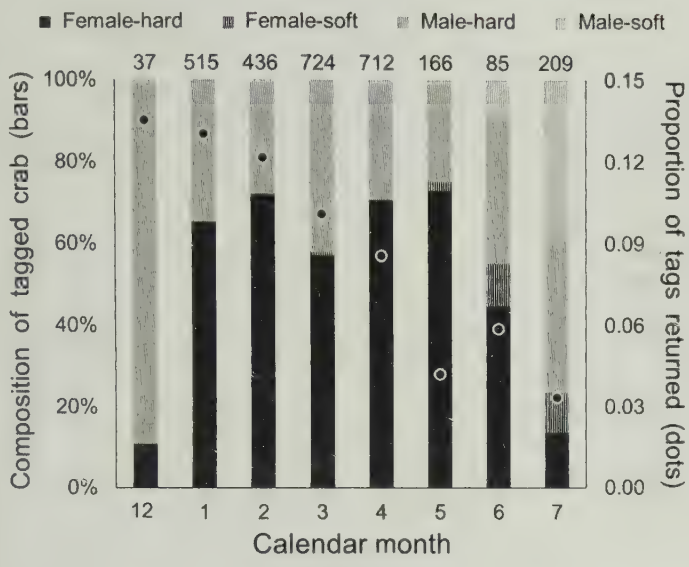

Figure 4

Composition of Dungeness crabs (*Cancer magister*) that were tagged and released during commercial fishing trips off Oregon between October 2012 and April 2014 and for which tags were returned, by combination of sex and shell hardness (bars), and proportion of crabs for which tags were returned (dots) by the numeric calendar month in which the tagged crabs were released (from December to July). The numbers above the bars indicate the total number of tags released by month.

higher return rates for noninjured crab than injured (all combined: 11% noninjured, 3% injured). This was consistent for both sexes (males 12% vs. 4%, females 7% vs. 0%); however, there were only 25 injured of tagged crab and the average reflex impairment score was higher for injured animals, suggesting that, as with the commercial fishery, the decrease in probability of return for injured crab was likely represented by the reflex impairment score.

Relative short-term survival

The ratios of short-term survival rates of condition 2 (score greater than 0) to condition 1 (score-0) crab were highly variable among release events for the tag-return study (Fig. 6) but indicated minimal differences in survival between conditions. Some release events indicated that condition-1 crab had higher survival than crab classified as condition 2, and others the opposite. Regardless, for all release events for females and hard-shell males, the overlapping CIs indicated no statistical difference between conditions. For soft-shell males, there was only one release event with enough data to calculate a relative survival rate. That event indicated survival was higher for condition-2 crab.

Ratios of relative short-term survival of condition-2 to condition-1 crab in the laboratory holding experiment indicated no difference between conditions in some cases and, in others, that condition -1 crab had higher survival. For all fisheries, the relative survival ratio for hard-shell males was either equal to or very close to 1, indicating no differences in survival between conditions. For females, 95% CIs of the ratios overlapped with 1 for the recreational fisheries, but the ratio for the commercial ocean fishery indicated higher survival for condition-1 crab. For both the commercial ocean and recreational bay by-boat fisheries, the ratios indicated higher survival for condition -1 soft-shell male crab than for condition-2 soft-shell male crab. The 95% CIs of these ratios, however, included a value of 1.

Relative long-term survival

Model results indicated that, for all release events where there were adequate sample sizes to complete the analysis, the intercept and variable coefficients were not significantly different from zero. When back-transformed from the logit scale and plotted, however, the intercepts were consistently at or above 0.5 (i.e., the proportion of tag returns from condition-2 crab were 50% or greater, even though there were higher numbers of tags released for condition-1 crab). The estimated slope coefficients for the majority of the release events, although not significant, were negative (i.e., the log-odds of a returned tag being from a condition-2 crab decreased over time). If significant, this would indicate a chronic difference in survival between conditions, namely that probability of a tag return, and therefore survival, for condition-2 crab could decrease over time relative to condition-1 crab. There were no consistent patterns, however, among release events that would signify an optimal monitoring duration beyond the 5 d "recovery period." Also, the lack of significance in the estimated model coefficients means there were no detected changes over time in the relative probability of a tag being returned from a condition-1 or -2 crab.

Evaluating the return to water

For the first drop experiment, 21 crab were dropped from 1 m, 22 from 3 m, and 20 from 8 m. There were only 7 soft-shell males and 6 soft-shell females dropped for all heights combined, and 81%, 73%, and 70%, respectively, by drop height were male. By drop height, 0% (1 m), 5% (3 m), and 45% (8 m) died within 5 d of holding. The one crab that died from the 3-m drop was a soft-shell female that had incurred both a broken leg and an autotomized leg from the drop. From 8 m, 6 of the 9 mortalities were male, and 3 were female (43% of males died, and 50% of females). All of the crab that died for this experiment, except one, had a cracked carapace as a result of the drop.

For the second experiment, a total of 18 crab were

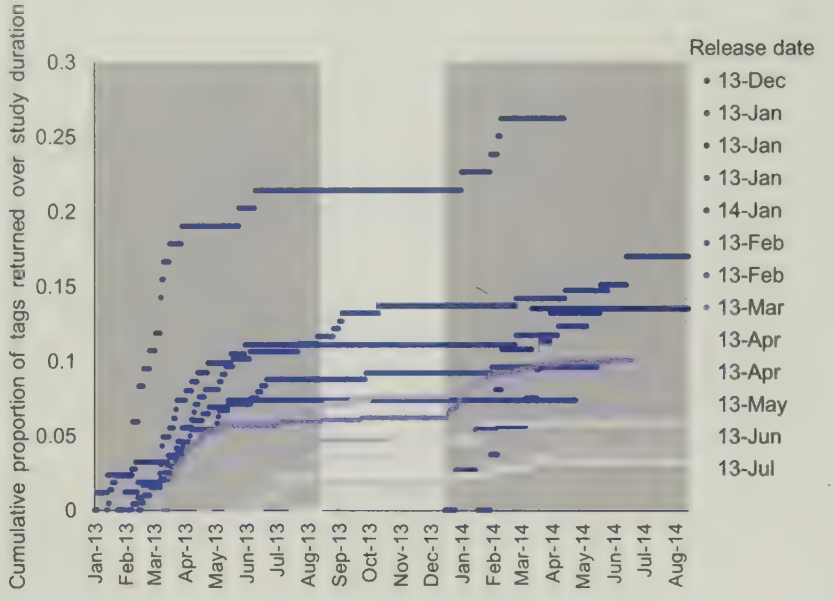

Figure 5

Cumulative proportion of Dungeness crab (*Cancer magister*) that were tagged and released during commercial fishing trips off Oregon between October 2012 and April 2014 and whose tags were returned over the duration of the study, by release event (year and month released). Darker symbols indicate release events earlier in the fishing season, fading in color as the season advances (from December to July). The gray background indicates when the fishing season was open.

dropped from 3 m, 18 from 6 m, and 22 from 8 m. Respectively, 83%, 89%, and 82% were male; and only 1 soft-shell male and 3 soft-shell females were dropped for all heights combined. By drop height, 0% (3 m), 0% (6 m), and 14% (8 m), respectively, died within 5 d of holding. From 8 m, only males died (3 of 18 males compared to 0 of 4 females), and all dead crab had major carapace cracks.

Results from logistic regression indicated that mortality from the return to water is primarily influenced by whether or not the carapace cracks as a result of the drop. Whether a carapace cracked was closely linked with drop height and whether or not the crab was in water before being dropped. Both experiments combined, by height, revealed that 0% (1 m), 0% (3 m), 6% (6 m), and 33% (8 m) of crab had cracked carapaces as a result of the drop, indicating an increased probability of cracking as drop height increases. Considering whether or not the crab was left out of water before it was dropped, for just the 8 m drop, 55% of those left out of water (experiment 1) and 14% of those kept in water (experiment 2) had cracked carapaces. These results suggest that mortality could be linked with whether or not a carapace cracks, which is potentially influenced by both drop height and whether or not a crab is left out of water before being returned to water. Further investigation is needed to determine the role of shell hardness in inducing mortality.

Discussion

Patterns in delayed discard mortality based on tag-returns

Commercial ocean fishery Probability of tag return for the commercial ocean fishery was influenced by reflex impairment score, sex, shell hardness, carapace width, and time of release in relation to the opening of the fishing season. Males had higher tag-return rates than females and, for both sexes, hard-shell crab had higher rates than soft-shell crab. Similar percentages of score-0 crab were tagged for each category, which suggests that differences in returns were not influenced by discrepancies in composition of tagged crab by score, but rather by differences in survival. The few returns of tagged crab with scores greater than 0 (36) limited an analysis of return trends by individual score. However, decreasing returns as scores increased for females and soft-shell males and lower scores, on average, for returned crab are consistent with the idea that crab with higher reflex impairment scores had higher rates of mortality. Moreover, lower average scores for noninjured crab compared with injured crab supports the assumption that injury is reflected in the score. These tag-return patterns mirror results from the laboratory study in which delayed discard mortality rates were dependent upon level of reflex impairment (increasing mortality with higher scores), sex (higher mortality for females), and shell hardness (soft-shell males had higher mortality than hard-shell males; few soft-shell females were captured requiring soft- and hard-shell females to be combined for the laboratory study).

Patterns in tag-return rates indicated potential bias due to carapace width and month of release. For both sexes, the frequency of returns was higher for crab with larger carapace widths than for smaller tagged crab, possibly indicating that size affected the likelihood of return. This could be due to the fact that fishermen immediately discard crab with carapaces that are clearly smaller than the legal-size requirement without evaluation. In addition, a tag was more likely to be returned if tagged and released closer to the beginning of the season, likely because effort is highest at this time (i.e., there are more vessels on the water and, therefore, more pots pulled) and decreases over the fishing season.

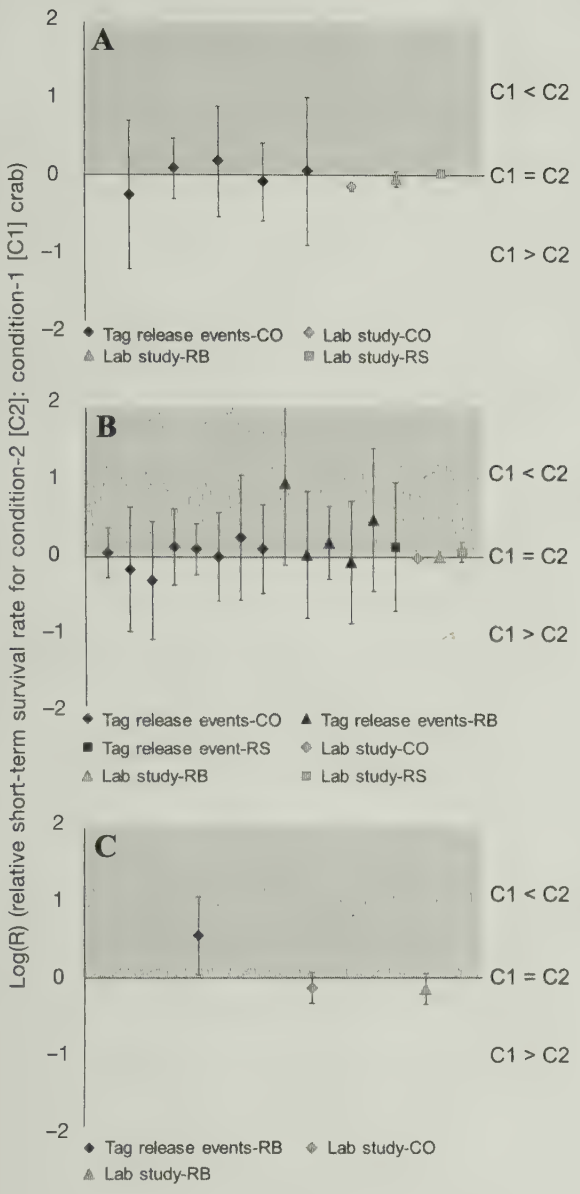

Figure 6

The relative short-term survival rates of Dungeness crabs (*Cancer magister*) collected off Oregon between February 2012 and April 2014 and classified as condition 2 (C2: reflex impairment score >0) or as condition 1 (C1: score=0) for tag release events and the laboratory holding study by fishery (commercial ocean fishery [CO] and recreational fisheries in Yaquina Bay, by boat [RB] and shoreside [RS]). **(A)** females, **(B)** hard-shell males, and **(C)** soft-shell males. Hard- and soft-shell females were combined owing to low numbers of the latter caught and, therefore, held or tagged). Note that the upper confidence limit (2.07) for the first RB tag release event for hard-shell males exceeded the axis rule.

Recreational fisheries Patterns in tag-return data from the recreational bay fishery from a boat are similar to mortality rate patterns from the laboratory-holding study for this fishery in that reflex impairment score and shell hardness were weak predictors, and rates were lower than those of the other fisheries. For the laboratory study, the most important predictor of delayed mortality was whether or not the crab had any missing reflexes (a binary response). Mortality rates for crab were statistically indistinguishable by the level of impairment. However, modeling outcomes for this fishery could have been influenced by the low numbers of crab with missing reflexes and the high proportion of hard-shell males caught, and, therefore, held in captivity, which had a higher survival rate than females and soft-shell crab from the commercial fishery. Also similar to trends in the laboratory study, noninjured crab had a higher return rate than injured crab. However, the significance of the relationship between the probability of tag return and injury was difficult to measure given the small number (35) of injured crab that were tagged and released. As in the commercial fishery, patterns in tag returns suggest that carapace width and sex may also have influenced return rates with this fishery. The frequency of returns was higher for crab with larger carapaces compared with the size frequency of those tagged. Also, overall return rates for females were lower than those for males. Although this result could reflect reduced survival for females that went undetected in the laboratory-holding study, it could also be indicative of a bias caused by fishermen and attributable to the sex of the crab. As they do with small crab, fishermen instinctually discard females without much inspection, while males are measured to determine their legal status. In measuring the crab, fishermen have more opportunities to observe the tag.

Mortality rates were not estimated for the recreational shoreside fishery in the laboratory holding study. However, Yochum et al. (2017) found that rates were likely more similar to those estimated for the commercial ocean fishery than the recreational bay fishery from a boat (Yochum et al., 2017). Tag returns for the recreational bay shoreside fishery, like the commercial sector, indicated that the probability of return is likely influenced by reflex impairment score, sex, shell hardness, and carapace width. This notion is consistent with laboratory findings, which indicated that mortality rates for the commercial ocean fishery could likely be applied to the shoreside fishery. With respect to bias, as with other fisheries, return rates were higher for larger crab. There were no clear temporal patterns; however, sample sizes were small for each release event.

Efficacy of tag-return methods for research on discard mortality

There are limitations when using tag-return methods to evaluate discard mortality for a low-impact fishery (i.e., one where, for the majority of animals, the stress-

ors do not impair the reflexes). In analyses, in absence of a control to evaluate score-0 crab and with low numbers of reflex-impaired animals, crab with scores greater than zero were combined. Therefore, crab with low mortality probabilities (e.g., score-1) were mixed with moribund animals (score-6), which obfuscated a clear comparison of crab with different levels of impairment and prevented the detection of statistical differences in relative short- and long-term survival rates between the laboratory and tagging studies.

These limitations highlight the importance of being able to tag and recapture a sufficient number of animals for each reflex impairment score when executing a tag-return study using the RAMP approach. Hueter et al. (2006), in describing the methods used here to look at relative short-term survival, tagged a minimum of 365 animals per condition. For the commercial ocean fishery, which had the highest number of crab with scores greater than 0, of the 5594 crab assessed overall, only 202 had reflex impairment scores greater than 1 (129 score-2; 46 score-3; 14 score-4; 5 score-5; and 8 score-6; Yochum et al., 2017). These sample sizes are even smaller when divided into subcategories for sex and shell hardness, and when the lower-impact fisheries are considered. Moreover, the requirement of tagging a sufficient number of soft-shell crab becomes logistically impractical because the highest return rates are linked with release events early in the fishing season, a time when there are few to no soft-shell animals.

The efficacy of applying a tag-return approach for discard mortality research is also linked with the extensive list of factors that determine whether or not a tag will be returned. For this study, these included natural mortality, fishing-induced mortality (both retention and handling-induced mortality if a tagged animal is recaptured and released without the tag being observed), catchability, molt failure attributed to the tag, tag loss, tag-induced mortality, and reporting rate. Each of these factors is a potential source of bias in tag-return rates. In the case of Dungeness crab, natural mortality, for example, differs for crab that are and are not molting (Zhang et al., 2004). In addition, fishing-induced mortality must be considered when evaluating soft-shell crab that, after a period of time, become hard and recruit back into the fishery, or when evaluating sublegal crab that become legal size after molting during the study period. Moreover, different catchabilities could apply to recently molted male crab (Taggart et al., 2004), female crab based on whether or not they are egg-bearing (Swiney et al., 2003), and crab with different reflex impairment scores if a reduction in vitality affects a crab's inclination to eat and therefore enter a pot. Also, for the commercial fishery, there are temporal and spatial patterns in fishing practices (Gotshall, 1978; Barry[10]) that could affect tag return rates differently. The majority of effort and landings for the commercial Dungeness crab fishery occurs shortly after the season opens in December and during the first 2 months, after which fishermen often switch to an alternative fishery (Didier, 2002; Goblirsch and Theberge[11]). Because of this temporal trend, crab tagged and released near the beginning of the season (or crab at large during multiple season openings) have a higher chance of being observed than those tagged toward the end of the season when fishing effort is lower. The physical presence of the tag may also affect return rates given its potential to impede molting, to be lost, or contribute to mortality. In addition, tag reporting is potentially dependent on successful and extensive outreach, and the willingness and ability of fishermen to participate (Pollock et al., 2001). Finally, conducting a tag-return study on discarded animals can be challenging because they are less likely to be inspected than retained animals. Furthermore, some fishermen reported that, because female and sublegal-size male crab are not allowed to be retained, they were not sure if they were supposed to remove the tag or leave it in place. However, if sufficient tag returns permit relative analysis by score for a single release event, then many of the aforementioned variables of concern become irrelevant.

Reliability of estimating mortality under captive holding conditions

To address the goal of the field validation in ascertaining the accuracy of the laboratory-based mortality rates estimated by Yochum et al. (2017) for Dungeness crab, we conclude that, although direct rate comparisons were not possible, similar patterns in mortality- and tag return- rates from the 2 studies lend support to the reliability of the laboratory-generated rates. However, results from the tagging study suggest that laboratory-based mortality rates for discarded females should be evaluated to determine whether there is a discrepancy between hard- and soft-shell crab. In addition, mortality would be underestimated if the laboratory-based commercial rates were applied to a shoreside fishery where the discarded crab fell more than 6 m (and potentially less). With respect to chronic mortality, for all fisheries, there was no conclusive evidence that suggests mortality rates were underestimated in the laboratory study because of short-term holding.

In general, trade-offs between laboratory holding and tag-return for estimating discard mortality rates depend on the overall objectives of the study, logistic constraints, and the level of impairment caused by the stressor(s) being studied. For our 2 studies, the laboratory-based RAMP approach was superior in its ability to quantify mortality rates and to detect significant differences among several variables. Regardless, the tag-return study identified important influences on mortality and allowed increased collaboration and outreach in the fishing community. In addition, advantages of the tag-return approach over captive holding include the fact that the conditions with the former

[11]Goblirsch, G., and S. Theberge. 2008. Traps. Sea Grant Oregon ORESU-G-08-002, 2 p. Oregon State Univ., Corvallis, OR. [Available from website.]

approach more closely mimic actual fishing stressors and a more natural environment after release, and reduce handling (transporting the animals from the fishing vessel to the laboratory and maintaining them in tanks). For the Oregon Dungeness crab fisheries, these approaches, used together, provided a more comprehensive evaluation of what affects survival of discarded crab. In both studies, sample size is highlighted as a critical consideration when applying the RAMP approach to a low-impact fishery.

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The influence of nutrients from carcasses of sea lamprey (*Petromyzon marinus*) on larval growth and spawner abundance

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Abstract—Migrations of anadromous sea lamprey (*Petromyzon marinus*) from marine ecosystems serve as vectors of nutrients into freshwater food webs. Larval sea lamprey reside in streams for 6–8 years as deposit feeders before metamorphosing into juveniles and migrating to the ocean. Previous work has shown that carcass nutrients, which result from the death of adult lamprey after spawning, increase stream productivity and are consumed by larvae. This may increase larval growth rates and enhance earlier metamorphosis. We examined the sensitivity of life-history parameters and influence of nutrients from carcasses of sea lamprey on the age and growth of larval conspecifics with a deterministic stock-recruitment model. We hypothesized that variability in growth among larval populations is productivity mediated and we compared modeled populations in which larvae receive added growth benefits from carcass nutrients with populations that do not. The results of our simulation indicate that increases in larval growth and lower age at metamorphosis over time lead to an increase in spawner abundance. Increased growth rates may also improve fitness and bolster subsequent spawning stocks. Our research characterized 2 potential ecosystem states, one in which larval sea lamprey benefit from adult conspecifics and another in which the larvae do not.

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Anadromous fish link freshwater and marine ecosystems through the seaward emigration of juveniles and subsequent immigration of adults. These adult fish serve as vectors of marine-derived nutrients into freshwater via metabolic waste, gametes, and the carcasses of dead spawners (Gende et al., 2002; Nislow and Kynard, 2009; Näslund et al., 2015). The resulting nutrients may have a bottom-up effect on freshwater systems through the stimulation of primary and secondary production (Wipfli et al., 2003; Kohler et al., 2008; Weaver et al., 2016). Concurrently, a proportion of liberated nutrients may be assimilated by larval and juvenile fish that reside in freshwater before their migration to the ocean (Lang et al., 2006; Kiernan et al., 2010; Rinella et al., 2012; Weaver, 2017). Unfortunately, dam construction, habitat modification, and overfishing have reduced or eliminated many populations of anadromous fish (Saunders et al., 2006; Sheer and Steel, 2006; Limburg and Waldman, 2009), by severing linkages between freshwater and marine ecosystems. Reduced connectivity diminishes the exchange of energy and nutrients and significantly alters stream food-web structure and productivity (Lamberti et al., 2010). The resulting decrease in adult returns to freshwater systems may, therefore, decrease the supply of nutrients to these systems.

Anadromous populations of sea lamprey, (*Petromyzon marinus*) subsidize Atlantic coastal freshwater systems during the spring with pulses of marine-derived nutrients (Nislow and Kynard, 2009; Weaver et al., 2015). Sea lamprey spend 1–2 years in the ocean as a top parasitic predator of marine vertebrates (Silva et al., 2014) before migrating into temperate Atlantic coastal freshwater rivers and streams. There they mature, construct nests, spawn, and subsequently die (Beamish, 1980). Their carcasses release marine nutrients to the freshwater environment. During summer, rising water temperatures and increased pho-

toperiod stimulate primary production and increase the metabolic demand of consumers, including young-of-the-year fish and macro-invertebrates (Hall, 1972; Gustafson-Greenwood and Moring, 1990). The death of sea lamprey and the nutrients from their carcasses can alleviate nutrient limitations of streams and increase productivity to the overall benefit of freshwater communities (Weaver et al., 2016).

Carcasses of sea lamprey may directly benefit conspecifics. After hatching, larval sea lamprey burrow into fine substrate and reside in freshwater as deposit-feeding detritivores (Hardisty and Potter, 1971; Evans and Limburg, 2015). In a recent study, Weaver (2017) provided evidence of larval assimilation of nutrients from adult carcasses by documenting enrichment of the ^{13}C isotope among individual fish collected near carcasses. Larval sea lamprey that receive these nutrient subsidies may grow faster than larvae without access to such nutrients. During summer, larvae initiate metamorphosis, a nontrophic period characterized by a series of physical and physiological changes and arrested somatic growth and feeding (Youson, 1980; Youson and Manzon, 2012). After several months, the juveniles (macropthalmia) migrate toward the ocean to begin feeding as parasites (Potter et al., 1978). Thus, the accrual of a surplus of lipids (i.e., energy) during the freshwater larval period is critical for both the developmental "decision" to metamorphose and for the survival and migration of newly metamorphosed lamprey (Lowe et al., 1973).

Freshwater productivity can directly influence growth rates and drive population dynamics of fish populations. Although data that directly link productivity to growth rates are absent for sea lamprey, there is strong evidence of a correlation. The time from the larval period to metamorphosis, for example, has a range of 2–14 years among sea lamprey populations in freshwater of varying productivity (Manion and Smith[1]; Beamish, 1980; Potter, 1980; Purvis, 1980; Beamish et al.[2]; Morkert et al., 1998; Quintella et al., 2003). Larval growth rates and age at metamorphosis may also be influenced by stream productivity (Potter, 1980; Purvis, 1980; Dawson et al., 2015). Temperature, stream conductivity, and dissolved solids (which are proxies for productivity) were found to be significant predictors of growth rate (Holmes, 1990; Young et al., 1990; Griffiths et al., 2001). Among tributaries in the Great Lakes, the first occurrence of metamorphosis of sea lampreys ranges from age 2 in faster growing populations to age 7 in slower growing populations (Purvis, 1980; Morkert et al., 1998). This variability in the duration of the larval period and initiation of metamorphosis may be influenced by the influx of nutrients from the mortality of postspawning adult sea lamprey. This influx, in turn, may create an alternative stable state that reinforces production of spawning adults and promotes population persistence (Kéfi et al., 2016).

We assessed the theoretical influences of carcass nutrients on larval sea lamprey, with the assumption that growth and subsequent metamorphosis of larvae are linked to freshwater productivity. We hypothesize that carcass-mediated productivity may shift the age at which larvae undergo metamorphosis. We used data and values from the literature to construct a heuristic model and probed the sensitivity of various life-history parameters on the growth and metamorphosis of larvae. We compared a hypothesized scenario in which carcass nutrients from adult sea lamprey had no effect on larval growth to a scenario in which increases in productivity mediated by carcasses increased growth. Finally, we explored theoretical effects of changes in metamorphosis on demographic (age) structure of larval populations.

Materials and methods

Population modeling

We used data and values of life-history parameters obtained from scientific literature to create a deterministic stock-recruitment model with the software STELLA[3], vers. 10.0.6 (isee systems, Inc., Lebanon, NH). Our model had 3 major parts: 1) a recruitment model; 2) a growth model; and 3) a nutrient feedback model (Fig. 1). The model was designed to capture the entire life history of sea lamprey beginning with larval recruitment in freshwater, metamorphosis and migration to the ocean, ocean survival, migration back to freshwater, and subsequent death and nutrient deposition. We describe 2 populations: one in which larval growth rates are not influenced by returning adult sea lamprey (i.e., *unsubsidized* populations) and one in which larval growth rates are influenced by returning adult sea lamprey (i.e., *subsidized* populations).

Recruitment

We characterized recruitment in early life stages by using a Ricker stock-recruitment relationship (Ricker, 1975; Guy and Brown, 2007). A Ricker curve depicts an increase and then a decrease in larval recruitment with increasing numbers of spawning adults, a relationship that is characteristic of an increasing probability of nest superimposition that may be observed among species that construct nests (e.g., sea lamprey;

[1] Manion, P. J., and B. R. Smith. 1978. Biology of larval and metamorphosing sea lampreys, *Petromyzon marinus*, of the 1960 year class in the Big Garlic River, Michigan, Part II, 1966–72. Great Lakes Fish. Comm., Tech. Rep.30, 33 p. [Available from website.]

[2] Beamish, F. W. H., B. J. Morrison, L. A. Barker, and B. J. Wicks. 1998. Ecology of recruitment in sea lamprey. Great Lakes Fish. Comm., Proj. Compl. Rep. Summ., 22 p. [Available from website.]

[3] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

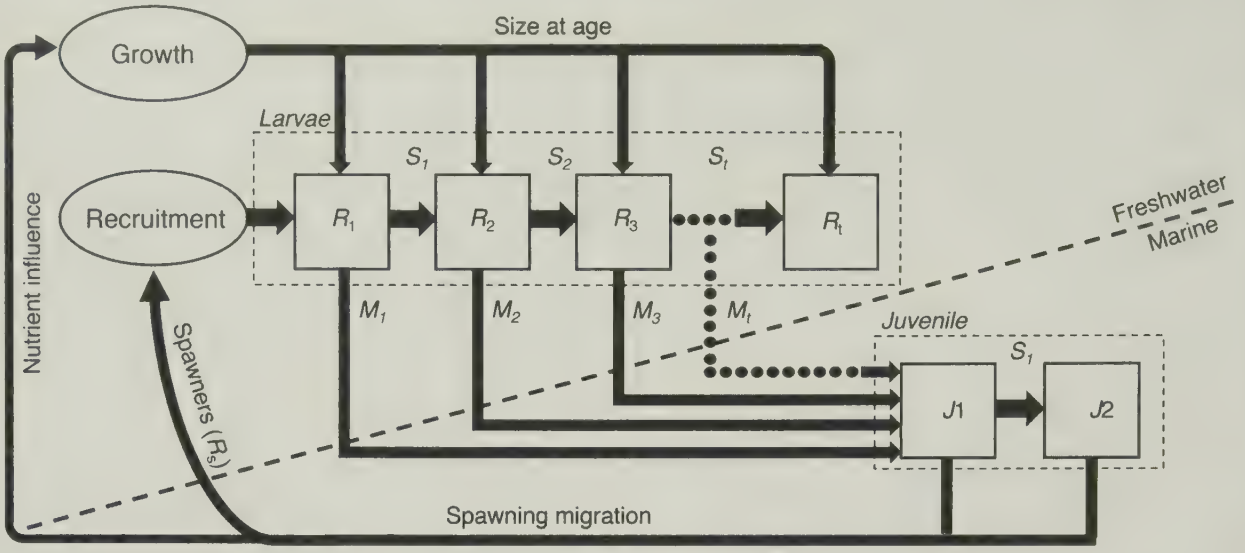

Figure 1

Conceptual diagram of population model used in this study to estimate freshwater larval recruitment (R_t) growth, survival (S_t), metamorphosis (M_t) and migration to the ocean, parasitic juvenile phase, and juvenile recruitment to freshwater (R_s) for sea lamprey (*Petromyzon marinus*). R_1–R_t represent ages of larval recruitment. S_1–S_t represent survival to the next age for either larvae or juveniles. J_1 and J_2 represent the number of juvenile lamprey spending one or two years at sea. The nutrient influence depicts the proposed effects of nutrients from sea lamprey carcasses on the growth of larval conspecifics.

Dawson, 2007; Dawson and Jones, 2009). We defined the recruitment relationship as

$$R_t = \alpha E e^{-\beta E}, \quad (1)$$

where R_t = recruitment of larvae at age class t;
E = the total number of eggs from female spawners;
α = the slope at the y-intercept of the stock recruitment relationship and describes survival at very low levels of E; and
β = the slope of the stock-recruitment relationship and describes the degree to which survival falls as E increases (i.e., carrying capacity).

We adjusted the α and β terms to obtain a stabilized population on the basis of the survival parameters used in the model (Table 1) and the desire to model a realistic carrying-capacity of adult spawners in a small stream (Gardner et al., 2012). We derived a value of β iteratively to obtain a stable population size of 4800 spawning adult sea lamprey for an area of suitable spawning habitat of approximately 4.8 ha (1 individual/10 m^2; Nislow and Kynard, 2009), which represents a realistic density of sea lamprey spawners in a third-order stream that was not impounded. We assumed an unequal sex ratio of 1.00:1.36 females to males for the total number of spawning adults (Beamish and Potter, 1975; Beamish et al., 1979). The value of E was calculated from the number of females with an average mass of 885.2 g (Beamish et al., 1979) and 233 eggs/g of mass (Hardisty, 1971; Table 1).

Freshwater larval growth

We permitted larvae to remain in freshwater for up to 12 years, which is within the range of the reported development period (Manion and Smith[1]; Beamish, 1980). We modeled growth of larval sea lamprey according to a von Bertalanffy (1938) function, defined as

$$L_t = L_\infty(1 - e^{-K(t-t_0)}), \quad (2)$$

where L_t = the length of the larvae at time t (years);
L_∞ = the theoretical maximum (asymptotic) body length;
K = the Brody growth rate coefficient per year that describes the decline in growth rate as individuals approach L_∞; and
t_0 = the theoretical age at which body length is zero (Guy and Brown, 2007).

We adopted the Ford–Walford method for estimating parameters of the von Bertalanffy growth function (Ford, 1933; Walford, 1946; Isely and Grabowski, 2007) by plotting L_t and L_{t+1}, transforming the von Bertalanffy growth model to follow a linear relation.

We used the plot of L_t and L_{t+1} to extract the intercept b from linear regressions with different K values ranging from 0.3 to 0.7, which were selected to represent a range of growth trajectories along a gradient of hypothetical streams of varying productivity. At K

Table 1

Settings for recruitment and life-history variables for a model that represents a population of anadromous sea lamprey (*Petromyzon marinus*).

Variable	Value	Source
Recruitment		
α	0.0014	Derived from this study
β	2.84×10^{-9}	Derived from this study
K	0.3–0.7	Modified from Quintella et al. (2003)
Eggs (β·g·mass^{-1})	233	Hardisty (1971)
Female adult mass (g)	885.2	Beamish et al. (1979)
Proportion of females	0.44	Beamish and Potter (1975), Beamish et al. (1979)
Mortality		
Larval mortality (M_{larv})		
Age 1	0.70	
Age 2	0.20	
Age 3	0.10	Adopted from Zerrenner (2001), Howe et al.[5]
Age 4	0.10	
Age 5	0.10	
Ages 6–12	0.10	
Metamorphosis (M_{met})	0.40	Best guess estimate
Juvenile (M_{juv})	0.40	Eshenroder et al.[6], Jones et al. (2003); Howe et al.[5]

values <0.3, simulated larval populations did not reach L_∞ within the designated age structure. We capped the range of K at 0.7, which was observed in larval populations by Quintella et al. (2003) in the Mondego River, Portugal, where larvae grew relatively quickly and achieved metamorphosis at age 4 or younger. We plotted K and b values and then extracted the linear equation to use as an intercept (b_w) to estimate the length of larvae. We then estimated the body length of an individual at t+1 as

$$L_{t+1} = L_t e^{-K + b_w}. \quad (3)$$

This method allowed us to manipulate K as a way of representing the influence of nutrient subsidies on larval growth. Estimated values of K obtained from the Ford–Walford plot were calculated as the inverse natural log of the slope. This method approximates but is not identical to those directly derived from the von Bertalanffy growth function (Isely and Grabowski, 2007).

To define the von Bertalanffy growth curve, we used an initial hatching length of 10 mm, a size adopted from 51-d posthatch larvae of Pacific lamprey (*Entosphenus tridentatus*) (Barron et al., 2016). We found reported total lengths (TLs) of larval sea lamprey before metamorphosis in a range from 120 to 200 mm (Manion and McLain[4]; Potter et al., 1978; Quintella et al., 2003), and we used a length of 200 mm TL as the value for L_∞. We defined a minimum K value of 0.3, which served as a baseline value for simulated unsubsidized populations. Subsidized populations had augmented K values that were calculated as a function of the number of returning adult spawners (see Eq. 7 in the *Nutrient feedback model* section).

We adopted the pattern of estimated annual interval larval mortality at age from Zerrenner (2001), Zerrenner and Marsden, 2005, and Howe et al.[5] (Table 1) for larval ages 1–12. We calculated larval survival to the next age class with the following equation:

$$N_{t+1} = N_t\,(1 - M_{larv})(1 - P_{met}), \quad (4)$$

where N_{t+1} = the number of larvae that are recruited to the t+1 age class;
N_t = the number in the current age class;
M_{larv} = the estimated larval mortality; and
P_{met} = the proportion of larvae that underwent metamorphosis and migrated out of freshwater.

Probability of metamorphosis

We modeled larval metamorphosis into the macropthalmic stage by using length and growth data from the

[4] Manion, P. J., and A. L. McLain. 1971. Biology of larval sea lampreys (*Petromyzon marinus*) of the 1960 year class, isolated in the Big Garlic River, Michigan, 1960–65. Great Lakes Fish. Comm., Tech. Rep.16, 33 p. [Available from website.]

[5] Howe, E. A., E. Marsden, and T. M. Donovan. 2004. Stage based population viability model for sea lamprey (*Petromyzon marnius*). Lake Champlain Basin. Prog., Tech. Rep. 43, 37 p. [Available from website.]

von Bertalanffy growth curve. Larvae that reached 160 mm TL were considered developed enough to undergo metamorphosis and migrate to the ocean on the basis of the midpoint of the range of lengths at which larvae begin metamorphosis (120–200 mm TL, see previous section). We estimated the number of individuals that underwent metamorphosis of each age class (N_{met}) with the following equation:

$$N_{met} = N_t\,(1 - M_{larv})P_{met}(1 - M_{met}), \quad (5)$$

where P_{met} = the probability of metamorphosis; and
M_{met} = the mortality associated with metamorphosis and migration to the ocean. M_{met} is poorly characterized (Hansen et al., 2016) but, for our purposes, was designated as 0.4 for individuals of all age classes.

Juvenile demographics

Juvenile sea lamprey typically spend 1–2 years at sea (Beamish, 1980). We calculated the number of juveniles spending a second year in the ocean as

$$J_2 = J_1\,(1 - M_{juv})(1 - P_{mat}), \quad (6)$$

where J_2 = the number of juveniles recruited to a second year at sea;
J_1 = the number of juveniles that have completed a full year at sea;
M_{juv} = the estimated juvenile mortality; and
P_{mat} = the proportion of individuals recruiting to maturity and returning to freshwater to spawn.

We calculated M_{juv} to be 0.40, by averaging estimates of survivorship of juvenile to adult spawners in the Great Lakes (Eshenroder et al.[6]; Jones et al., 2003; Howe et al.[5]; Table 1). We designated probabilities associated with juvenile P_{mat} after 1 and 2 years at sea as 0.5 and 1.0, respectively.

Nutrient feedback model

Carcasses of postspawn sea lamprey deposit organic carbon and inorganic nitrogen and phosphorous in freshwater streams (Weaver et al., 2015), and such deposits have been reported to influence stream productivity (Weaver et al., 2016). To test the effect of a hypothetical influence of carcass nutrients on larval growth, we allowed the Brody growth coefficient K, to vary as a function of the number of carcasses deposited in freshwater. This estimate of K served as a representation of the influence of organic and inorganic nutrients. Although K is a growth coefficient (which represents the rate at which growth slows as larvae approach L_∞) and not a growth rate per se, we used it as a proxy for productivity-mediated growth rate because L_∞ is held constant. Therefore, higher values of K mean individuals reach their maximum length sooner. We hypothesized that a nutrient feedback mediated through additions to the value of K would have a peak effect (an inflection point) followed by diminishing returns as the addition of carcasses increased. This relationship has been postulated or shown for many ecological systems (Kéfi et al., 2016) and effectively described with a logistic regression. During model simulations of populations receiving nutrient feedbacks, we assumed K values followed a logistic regression:

$$K = 0.3 + 1/(1 + e^{-(\gamma + \delta TS_t)}), \quad (7)$$

where γ and δ = parameters that influence how steeply the logistic function rises through a midpoint and the duration at which the midpoint occur, and
TS_t = the total number of adults returning to freshwater streams at year t.

Calculated values from the logistic equation were added to the baseline K value of 0.3 to depict the adjustment in growth rate for larvae in subsidized populations.

Model execution

We initially populated each larval and juvenile age class with arbitrary values and ran the unsubsidized model for 200 years, which served as a burn-in period to allow the population to stabilize. We took the final numbers of each larval and juvenile age class and reseeded the starting model with those values. We estimated our unsubsidized population size at the point at which abundance remained constant over a 200-year period. We then reran the model with larval growth influenced by the number of returning adult spawners as reflected by varying values of K (Eq. 7) and examined the resulting changes in demographics for the subsidized population.

Model sensitivity

We gauged the local sensitivity of mortality, M_{larv}, M_{met}, M_{juv}; the parameters α, β, and K of unsubsidized populations; and the γ and δ logistic regression parameters for manipulating K in subsidized populations. We applied a 1% increase in selected parameters on the number of total spawners in the stabilized population. Sensitivity (S) of parameters for number of total spawners was calculated as

$$S = \frac{(R_a - R_n)/R_n}{(P_a - P_n)/P_n}, \quad (8)$$

where R_a = the result for the altered variable;
R_n = the result for the unaltered variable;
P_a = the altered parameter; and
P_n = the nominal parameter (Haefner, 2005; Bailey and Zydlewski, 2013).

Model output was deemed "sensitive" to the parameter if $|S| > 1.00$.

[6] Eshenroder, R. L., R. A. Bergstedt, D. W. Cuddy, G. W. Fleischer, C. K. Minns, T. J. Morse, N. R. Payne, and R. G. Schorfhaar. 1987. Great Lakes Fishery Commission Report of the St. Marys River Sea Lamprey Task Force, 35 p. [Available from website.]

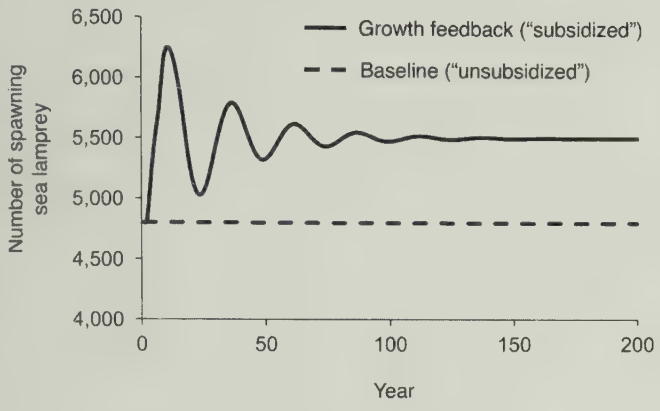

Figure 2

Number of spawning sea lamprey (*Petromyzon marinus*) that return to freshwater from the ocean in baseline unsubsidized model populations (dashed line) in which there are no effects of nutrients from carcasses of sea lamprey on the growth of larvae and changes in spawner abundance from subsidized model populations (solid line). The model for subsidized populations manipulates growth to account for the effect (or growth feedback) from nutrients released from carcasses.

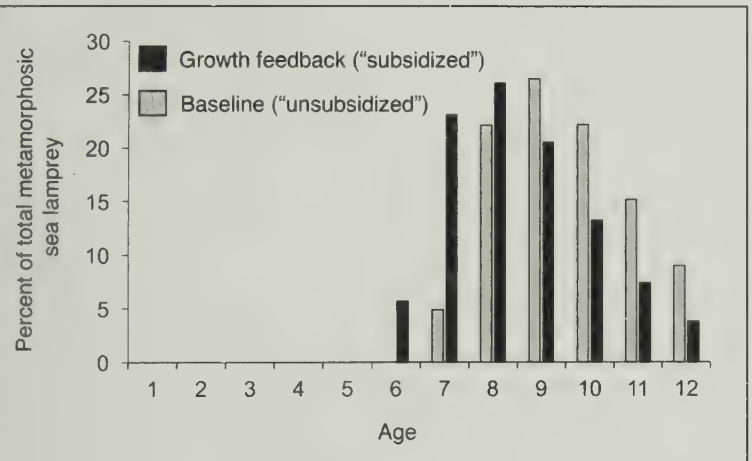

Figure 3

Percentage of total number of metamorphosic sea lamprey (*Petromyzon marinus*) for each age class in baseline unsubsidized model populations (gray bars) in which there are no effects of nutrients from carcasses of sea lamprey on larval growth, and corresponding changes in metamorphosic sea lamprey for each age class in subsidized modeled populations (black bars). The model for subsidized populations manipulates growth to account for the effect (or growth feedback) from nutrients released from carcasses.

Results

The population model was adjusted to simulate unsubsidized populations of total spawners at approximately 4800 individuals (Fig. 2), which is a reasonable estimate of spawner carrying capacity in a small, third-order stream. This number was used as the starting population for the simulation of subsidized populations with the incorporation of growth feedback. Subsidized populations of total spawners were variable for 100 years, then began to stabilize at a population size of approximately 5500 individuals, indicating a 12% increase in adult returns (Fig. 2).

We simulated changes in the distribution of age classes when larvae achieved higher growth rates from the input of nutrients from adult carcasses. When we assumed no feedback, >95% of all metamorphosed larvae were 8 years or older (Fig. 3). When we assumed nutrient feedback, larval populations shifted toward younger age classes. Approximately 30% of all metamorphosed larvae were younger than 8 years. The shifts in age at metamorphosis toward younger individuals correspond with the manipulations of age at length in the Von Bertalanffy growth model (Fig. 4). Results from the model indicate higher growth rates among the subsidized populations that allowed larvae to reach the minimum length at metamorphosis (160 mm TL) at an earlier age in contrast with results for unsubsidized populations that reached the minimum length at metamorphosis at relatively older ages.

The results of our sensitivity analysis indicated that age-1 larval mortality was relatively sensitive to change ($|S|>1.00$; Table 2). Generally, we found that increases in larval mortality resulted in lower returns of adult spawners and, conversely, that reduced larval mortality resulted in increases in the number of total spawners. Total modeled spawner abundance was inversely influenced by increases in mortality related to larval metamorphosis and the juvenile phase in the ocean; however, these parameters were less sensitive to change. Consistent with the role of the 2 constants in the Ricker function, α was positively associated with larval recruitment and β, which delineates carrying capacity, was negatively related. Neither of these parameters was deemed sensitive on the basis of our a priori sensitivity threshold (1.00), although both sensitivities approached the measure. Among subsidized populations, we found that changes in γ and δ parameters resulted in larger annual fluctuations in the number of total spawners and potentially prolonged the time necessary for populations to stabilize, but we did not find these parameters to be highly sensitive with respect to spawner abundance in the stabilized population.

Discussion

We constructed a deterministic model to illustrate the complex life history of sea lamprey, and the manipula-

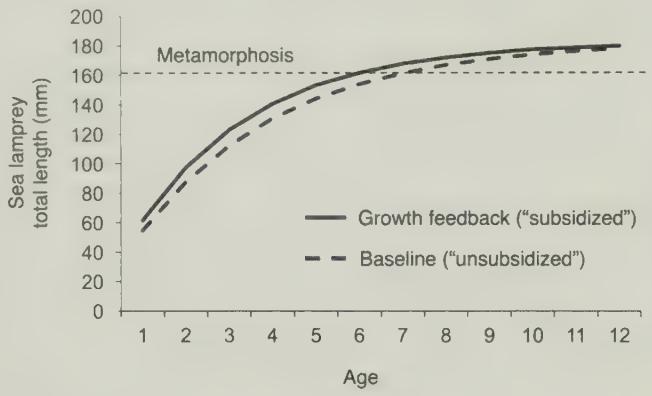

Figure 4

Age at length of larval sea lamprey (*Petromyzon marinus*) from a modeled von Bertalanffy growth curve in baseline unsubsidized model populations (dashed line) in which there are no effects of nutrients from carcasses of sea lamprey on the growth of larvae and changes in age at length in subsidized model populations (solid line). The model for subsidized populations manipulates growth to account for the effect (or growth feedback) from nutrients released from carcasses.

Table 2

Sensitivity (S) of the total number of returning, spawning sea lamprey (*Petromyzon marinus*) determined from stabilized model runs to a 1% increase in model parameters. Variables include larval mortality at age (M_{larv}), mortality at metamorphosis and time of migration to the ocean (M_{met}), juvenile mortality (M_{juv}), α and β parameters of the Ricker stock-recruitment relationship, and γ and δ logistic growth parameters of the nutrient feedback model. $|S|$ values above 1.00 were deemed sensitive and are indicated in bold.

Parameter		Nominal value	S
Recruitment	α	0.0014	0.833
	β	2.84×10^{-9}	−0.958
Mortality	M_{larv1}	0.74	**−1.895**
	M_{larv2}	0.07	−0.208
	M_{larv3}	0.05	−0.062
	M_{larv4}	0.09	−0.062
	M_{larv5}	0.12	−0.062
	M_{larv6}	0.10	−0.062
	M_{larv7}	0.10	−0.062
	M_{larv8}	0.10	−0.062
	M_{larv9}	0.10	−0.062
	M_{larv10}	0.10	−0.042
	M_{larv11}	0.10	0
	M_{larv12}	0.10	0
	M_{met}	0.60	−0.521
	M_{juv}	0.413	−0.708
Logistic growth	γ	−4.0	−0.563
	δ	1.0×10^{-4}	0.273

tion of model parameters allowed us to explore potential nutrient feedbacks between freshwater and marine ecosystems. Previous research has shown increases in freshwater productivity from carcasses of sea lamprey and assimilation of carcass nutrients by larval conspecifics (Weaver et al., 2016; Weaver, 2017). Results from our model indicate the potential role of carcass nutrients in stimulating larval growth and lowering the age at metamorphosis as a result of higher productivity. This model clearly illustrates the critical importance of nutrient exchange among anadromous fish between freshwater and marine systems, an exchange that is likely to result in population-level changes.

We hypothesized that recruitment dynamics of sea lamprey are driven by changes in in-stream primary production, but recruitment may also be shaped by density-dependent factors (e.g., prey abundance and competition; Klanderud, 2010), independent processes (e.g., temperature or flow; Tonkin et al., 2017), or a combination of both (Jónsdóttir et al., 2013). Juvenile sea lamprey in the ocean function as parasitic predators and their successful recruitment may, therefore, respond to an additional suite of biotic and abiotic factors, including less obvious factors related to the population dynamics of their hosts.

We show that changes in productivity may influence population demography, but other life-history attributes may be affected as well. For example, the sex-ratio of larval populations in more productive waters may become skewed toward females (Johnson et al., 2017), a shift that conceivably is a result of the addition and availability of carcass nutrients. Furthermore, one male may mate with several females (Beamish, 1980; Gardner et al., 2012), and recruitment dynamics may be further influenced by populations that are subsidized by carcass nutrients. Results from our model also indicate that population demographics may have an even farther reaching influence that could extend to other species and across ecosystems. High densities of larval sea lamprey may reduce individual growth rates and survival and extend the duration of the larval period and hence delay metamorphosis (Morman, 1987; Murdoch et al., 1992). Established populations that are at or near carrying capacity likely experience slower growth that is reflective of limited resources. Conversely, low densities of larvae, characteristic of populations facing impaired migratory access and thus fewer adult returns, may show higher growth rates among all cohorts (Purvis[7]; Torblaa and Westman, 1980; Morman, 1987). Models that do not account for density-dependent growth may not accurately capture associated

[7] Purvis, H. A. 1979. Variations in growth, age at transformation, and sex ratio of sea lampreys reestablished in chemically treated tributaries of the upper Great Lakes. Great Lakes Fish. Comm., Tech. Rep.35, 36 p. [Available from website.]

changes in population dynamics, including the recovery or re-establishment of fish populations (e.g., salmonids; Vincenzi et al., 2012).

We assumed that the addition of nutrients from mortality of postspawning adult sea lamprey (i.e., changes in productivity) influences the variability associated with growth and metamorphosis of larval sea lamprey. In reality, larval metamorphosis is dependent upon many different biological factors (e.g., lipid accrual; Lowe et al., 1973) and variation in environmental conditions that extend beyond productivity alone. Some of these factors have been thoroughly explored among other anadromous fish, especially salmonids, and may have implications for population demographics and persistence of sea lamprey. Anadromous salmon parr, for example, grow in freshwater before becoming smolts, a process characterized by a series of energetically demanding physical and physiological changes (McCormick et al., 1997). Research has shoen that higher water temperatures provide parr with more opportunities for growth, up to an optimal temperature after which growth is likely reduced, and this growth may result in earlier smoltification (Zaugg and McLain, 1976; Thorpe et al., 1989). Nutrients from carcasses of sea lamprey stimulate productivity during spring, a critical period of temperature-driven increases in metabolism for fish facing potential limitations in resources (Hall, 1972; Weaver et al., 2015; Weaver et al., 2016). Therefore, salmon parr that are subsidized directly and indirectly by these resources may benefit from a compensatory growth as fish approach the smolt stage (Guyette et al., 2013; Sigourney et al., 2013). This enhanced growth could potentially increase survival and reduce the number of years spent in freshwater before the young salmon successfully migrate to the ocean (Horton et al., 2009). Weaver (2017) showed nutrient assimilation of carcasses of adult sea lamprey by larval conspecifics, but because it has not yet been documented that carcasses contribute to larval growth, this process remains an important area for future study.

Many of the parameters used in our model are poorly documented in the scientific literature. Our model run for the unsubsidized, stabilized population was sensitive to several life-history and recruitment parameters. We used a sensitivity analysis to bracket what would be realistic values, with age-1 mortality being the most sensitive parameter among the tested variables. Population dynamics are largely governed by 3 demographic processes: recruitment, growth, and mortality (Hilborn and Walters, 1992), and results from our sensitivity analysis indicate that small changes in these processes can have substantial effects on both recruitment and the returning populations of spawning sea lamprey. Furthermore, the short-term dynamics of the model output are driven by the assumptions with using the Ricker curve, which may or may not accurately reflect the biology of sea lamprey. Other recruitment curves (e.g., the Beverton–Holt) may be biologically more realistic, but the long-term dynamics and stable states achieved do not differ. The results of our modeling highlight the need for more detailed life-history information for anadromous fish species like sea lamprey.

Anadromous sea lamprey are native to Atlantic coastal waters and are an important driver of nutrient cycling (Weaver et al., 2016). However, sea lamprey have garnered notoriety from their invasion into the Laurentian Great Lakes and their contribution to the decimation of native fish populations and altered food webs (Applegate, 1950; Bronte et al., 2003; Ricciardi, 2006; Great Lakes Fishery Commission[8]). Anadromous and landlocked populations exhibit similar life-history strategies, but the ecological implications have invoked differing fisheries management actions. Our modeling exercise was framed in the context of conserving anadromous Atlantic coastal populations, but these results may also have important implications for the way in which sea lamprey are managed in other systems. Sea lamprey in the landlocked Great Lakes are managed as a pest species, and recruitment dynamics may be influenced by the types of eradication and control methods used (Jones, 2007; Dawson and Jones, 2009). However, generally speaking, managers attempt to control invasive species with limited knowledge of their life history (Simberloff, 2003). A more complete understanding of the population dynamics of a species is critical for both population conservation and control strategies (Great Lakes Fishery Commission[8]). Our model is based on the hypothesis that nutrients from carcasses of sea lamprey increase larval growth rates and enhance earlier metamorphosis. This hypothesis is consistent with research in the Great Lakes, indicating that more productive waters contain faster growing larvae that reach metamorphosis at younger ages (Purvis, 1980; Morkert et al., 1998; Griffiths et al., 2001). Therefore, predictive models used for management and control measures of larval sea lamprey (Treble et al., 2008) may be more accurate with the incorporation of demographic shifts in populations of sea lamprey. The results from our model indicate the consequences of potential feedback mechanisms that may be relevant to decisions regarding management actions to conserve and restore ecosystem functions or control and eradicate an invasive species.

Currently, the focus of natural resource management has shifted toward ecosystem restoration (Palmer et al., 2014). Our model closes the hypothesized nutrient loop, and results from our model indicate a feedback process by which nutrients from carcasses of sea lamprey influence spawning stocks by subsidizing growth that may improve larval fitness (Hall, 1972; Hall et al., 1992). Globally, many anadromous fish species are threatened or imperiled (Limburg and Waldman, 2009) and our results indicate that current management strategies may need to consider energy and nutrient exchanges between ecosystems and the effects of these

[8] Great Lakes Fishery Commission. 2011. Strategic vision of the Great Lakes Fishery Commission 2011–2020. Great Lakes Fish. Comm., Misc. Publ. 2011-13, 29 p. [Available from website.]

exchanges on the life-history stages of the associated species. Broadly, our work highlights the importance of identifying and describing ecological functions among species that link multiple ecosystems.

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Gonadal maturation of the female smooth lumpsucker (*Aptocyclus ventricosus*)

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Abstract—Features of oogenesis, ovarian maturity phases, and fecundity of the smooth lumpsucker (*Aptocyclus ventricosus*) are described here for the first time. Gonadal development was examined by histological methods and the morphological features and size of germ cells at various stages was determined. These features were used to more accurately define morphological criteria of 7 histological and macroscopic maturity phases. The smooth lumpsucker is an iteroparous gonochoristic species with determinate fecundity, group-synchronous ovary organization, total spawning (release of 1 batch of eggs per breeding season), and external fertilization.

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The family Cyclopteridae is represented by about 16 genera and 28 species (Eschmeyer et al., 2017) that inhabit the cold waters of the northern hemisphere (Nelson et al., 2016). The lumpfish (*Cyclopterus lumpus*) is a commercial fish and the most studied member of this family (Goulet et al., 1986; Goulet and Green, 1988). Other members of this family have been studied less frequently, and information about their reproductive biology is fragmentary and scarce.

The smooth lumpsucker (*Aptocyclus ventricosus*) is a widely distributed marine fish species that is endemic to the North Pacific. It inhabits both near bottom and mid-water layers at depths ranging from 5 to 1700 m (Hart, 1973; Eschmeyer et al., 1983; Orlov and Tokranov, 2008). It is a common species that is ecologically relevant to local food webs throughout its distribution. It is a major consumer of gelatinous planktonic animals, such as jellyfishes and comb jellies (Yoshida and Yamaguchi, 1985) and an important source of food for some fish species, marine mammals, and birds (Kato, 1982; Orlov, 1997; Zeppelin and Ream, 2006; Anthony et al., 2008; Sinclair et al., 2008).

There is little information available on the spawning features (e.g., behavior, physical changes) or embryonic, and larval development of the smooth lumpsucker. It is only known that this species performs spawning migrations from deep water to coastal zones, where breeding occurs over a rocky bottom at depths shallower than 10 m. Eggs are demersal and adhesive and have an average diameter of 2.4 mm. The incubation time between fertilization and hatching is more than 40 d. Reportedly, females die after spawning and males continue to protect the egg clusters (Kyûshin, 1975; Ilynsky and Radchenko, 1992; Mecklenburg et al., 2002; Fadeev, 2005). Spawn-

ing times in different parts of the North Pacific vary but generally occur from February through May (Vinogradov, 1950). There are no data on the development of the reproductive system, oogenesis, ovary organization, and spawning pattern of this species.

Our main goal was to provide the first description of 1) oogenesis, 2) type of fertilization, 3) gonadal differentiation and development, and 4) an estimation of fecundity in female smooth lumpsuckers and to define both macroscopic and microscopic maturity phases. Macroscopic staging is much quicker and less expensive than histological staging; however, microscopic analysis provides a more precise determination of phases and was used to evaluate the efficacy of macroscopic maturity scales. Understanding the reproductive cycle of the smooth lumpsucker will help to elucidate the biology of other members of the Cyclopteridae family.

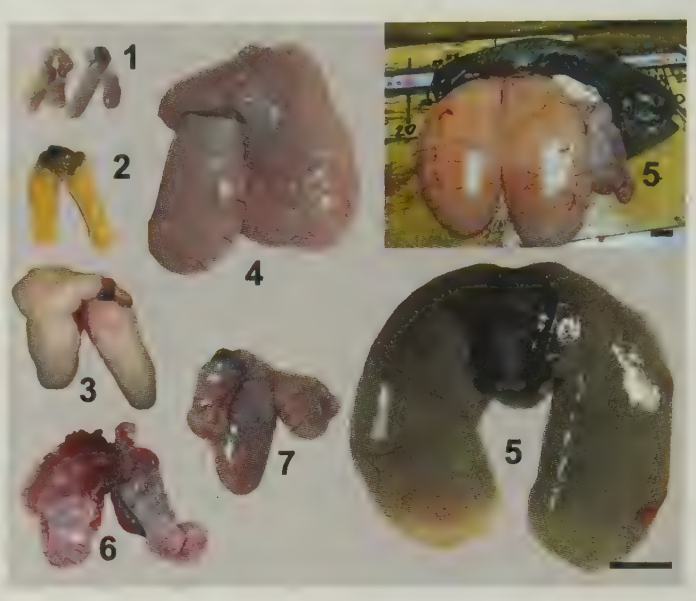

Figure 1

Photographs of ovaries of the smooth lumpsucker (*Aptocyclus ventricosus*) in different phases of gonadal maturation: 1) immature; 2) early developing; 3) developing; 4) spawning capable; 5) actively spawning subphase; 6) regressing; and 7) regenerating. The length of the scale bars represents 2 cm.

Materials and methods

Sampling for this study was carried out during an expedition on board of the research vessel *Professor Kaganovsky* (gross tonnage: 2508) of the Pacific Scientific Research Fisheries Center (TINRO-Center), Vladivostok, Russia, in the spring (16 March–30 May) of 2014. An RT/TM 57/360 midwater trawl net with 30-mm mesh was used. A total of 130 female smooth lumpsuckers were collected for analysis from the Sea of Okhotsk and near the southern Kuril Islands (43–60°N, 139–159°E). Total length (TL, in millimeters), body weight (BW, in grams), and gonad weight (GW, in grams) of each female were measured. The stomachs of smooth lumpsuckers typically were filled with water when the fish were brought on board, as is characteristic of this species and other Cyclopteridae (Ilynsky and Radchenko, 1992; Orlov, 1994). In this study, BW was measured after water had been expelled from the stomach. To analyze gonadal development, photographs were taken of the different maturity phases and then examined under magnification (Fig. 1). Gonadosomatic index (GSI) was calculated (Barrett and Munkittrick, 2010; Bahamonde et al., 2013) according to the following formula:

$$GSI = \frac{GW \times 100}{BW}, \quad (1)$$

where GW = gonad weight (in grams); and
BW = fish body weight (in grams).

Histological analysis was performed on 31 gonads that represent the different phases of development: 3 gonads for the immature phase, 12 gonads for the early developing subphase, 6 gonads for the developing phase, 4 gonads for the spawning-capable phase, 2 gonads for the regressing phase, and 1 gonad for the regenerating phase. Gonads were dissected and fixed in a 10% formalin solution in the field. The samples were then dehydrated, cleared with xylol, embedded in paraffin, sectioned (4 µm thickness), and stained with hematoxylin and Ehrlich's eosin. An Olympus BX45[1] microscope (Olympus Corp., Tokyo, Japan) and Leica DC 100 digital camera (Leica Microsystems,Wetzlar, Germany) were used for microscopy and photography. The image processing and data analysis program ImageJ, vers. 1.34e (Schneider et al., 2012) was used for measuring the diameters of oocytes and visualizing their structures. The ovarian phases of each gonad were classified on the basis of the most advanced oocyte stage observed in the histological sections according to the scale described in Brown-Peterson et al. (2011) (Table 1).

Absolute and relative fecundity were estimated by using 46 freshly caught females determined to be at the spawning-capable phase and at the actively spawning subphase by using the gravimetric method of Murua et al. (2003). A piece of ovarian tissue was taken from the median portion of the gonad from each specimen. The subsample of each ovary, representing 1.1–5.5% (about 10 g) of the GW, was weighed, and all advanced oocytes (diameter: 1.6–2.0 mm) in the subsample were counted by using an optical microscope MBS-9 (LZOS, Lytka-

[1] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

Table 1

Macroscopic maturity scale for ovaries of the smooth lumpsucker (*Aptocyclus ventricosus*), with corresponding histological gonadal phases and oocytes stages (Brown-Peterson et al., 2011). Histological features include primary growth (PG) oocytes; cortical alveolus stage (CA) oocytes; primary (Vtg1), secondary (Vtg2), and tertiary vitellogenic (Vtg3) oocytes; atretic (A) follicles or eggs; oocyte maturation (OM); germinal vesicle maturation (GVM); germinal vesicle breakdown (GMBD); and postovulatory follicles (POFs). GSI=gonadosomatic index.

Maturity phases	Main histological features of each phase	Main macroscopic features of each phase
Immature	Oogonia, PG	Ovaries small, translucent, gray, white, milky, or pink, occupy less than 1/5 of the body cavity. In some cases, ovary envelope is characterized by black color. GSI<0.6%.
Early developing subphase	PG, CA	Ovaries yellow, milky, pink, or reddish, occupy about 1/4 the volume of the body cavity. No eggs are visible to the eye. GSI 2.7–5.6%.
Developing	PG, CA, Vtg1, Vtg2	Ovaries opaque, orange, milky, pink, or reddish, occupy about 1/3–2/3 the volume of the body cavity. Small eggs are visible to the eye, with diameter <1 mm. GSI 3.7–39%.
Spawning capable	PG, CA, Vtg3, OM	Ovaries gray, milky, or pink, occupy about 2/3 the volume of the body cavity. Eggs are visible to the eye and had diameter >1 mm. GSI 31–45%
Actively spawning subphase	PG, GVM, GVBD, hydration, ovulation	Ovaries occupy all the volume of the body cavity, opaque, gray, or pink. Visible eggs (diameter >2 mm) are presented. Oocytes are 2 times larger than in the spawning-capable gonads. GSI 31–56%.
Regressing	POF, PG, some CA or Vtg, residual eggs present	Ovaries red or black, flaccid, with enlarged blood vessels. Gonads are reduced in size, occupy less than 1/3 of the body cavity. GSI 5.5–10.5%
Regenerating	PG, A, some CA, gamma/delta atresia and old POFs may be present	Ovaries occupy about 1/3 the volume of the body cavity, gray or reddish, with distinguished blood vessels. GSI 6%.

rino, Russia) at 8×2 zoom. Absolute (F_{abs}) and relative fecundity (F_{rel}) were estimated as

$$F_{abs} = \frac{n \times GW}{w}; F_{rel} = \frac{n \times GW}{w \times BW}, \quad (2)$$

where n = the number of advanced oocytes in subsample;
w = the weight of the subsample (in grams);
GW = the gonad weight (in grams); and
BW = the fish body weight (in grams).

Results

Immature ovaries were observed in the smallest females, which had a mean TL of 159.0 mm (standard deviation [SD] 55.2), a mean BW of 305.4 g (SD 228.0), and a mean GW of 6.2 g (SD 5.6). The most advanced germ cells in immature ovaries were represented by primary growth oocytes. Also observed were early primary growth (chromatin nucleolar) oocytes, which are characterized by a basophilic cytoplasm stained with hematoxylin and a large round nucleus with the nucleolus arranged at the periphery. Their diameters ranged from 46 to 101 µm (Fig. 2A). Advanced primary growth (perinucleolar) oocytes had diameters from 93 to 188 µm. Primary growth oocytes were characterized by the presence of oil droplets at the oocyte cytoplasm periphery. The GSI of the immature female was 3% (SD 0.6).

Gonads in an early development subphase were found in larger females, which had a mean TL of 220.5 mm (SD 39.9), a mean BW of 362.3 g (SD 150.7), a mean GW of 19.1 g (SD 9.7), and a mean GSI of 4% (SD 0.7). Cortical alveoli oocytes, as the most developed oocyte present, were diagnostic of this subphase. Their diameters at the early stage ranged from 218 to 359 µm and had a zona radiata width of 2–3 µm (Fig. 2B).

Gonads of the developing phase, observed in still larger females that had a mean TL of 257.2 mm (SD 35.1), a mean BW of 828.5 g (SD 193.6), were the most variable in terms of the size and weight of the gonads, and having a mean GW of 213.5 g (SD 142.5) and a

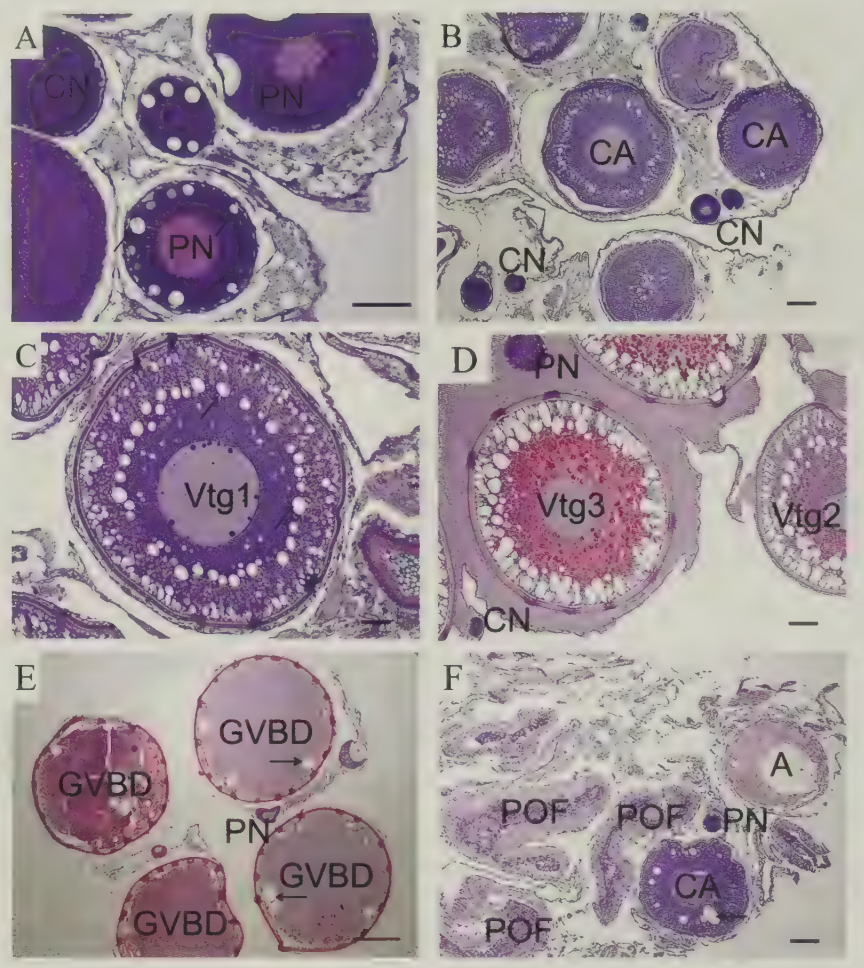

Figure 2

Photographs of ovaries of the smooth lumpsucker (*Aptocyclus ventricosus*) showing the microscopic characteristics of different gonadal phases: (**A**) immature; (**B**) early developing subphase; (**C**) developing; (**D**) spawning capable; (**E**) actively spawning subphase; and (**F**) regenerating. Microscopic characteristics include chromatin nucleolar (CN), perinucleolar (PN), cortical alveoli (CA), primary (Vtg1), secondary (Vtg2), tertiary vitellogenic (Vtg3), germinal vesicle breakdown oocytes (GVBD), postovulatory follicles (POF), atretic eggs (A), and oil droplets (arrow). The lengths of the scale bars represent (A–C) 50 µm, (D and F) 100 µm, and (E) 600 µm.

mean GSI of 28.9% (SD 7.6). The most advanced germ cells in this phase were primary and secondary vitellogenic oocytes, which increased in diameter because of increased yolk in the cytoplasm. Oocytes were from 360 to 448 µm, and the number of oil droplets increased during the later stages. In cortical alveoli oocytes, the zona radiata became thicker (7–9 µm), and delicate striations appeared. The process of yolk filling the cytoplasm began at the periphery and progressed toward the central areas of the oocytes, whose diameters ranged from 447 to 512 µm (Fig. 2C).

Females with ovaries at the spawning-capable phase had a mean TL of 263 mm (SD 45.9), a mean BW of 944 g (SD 186.4), a mean GW of 330 g (SD 131), and a mean GSI of 36% (SD 7.4). In the ovaries of these females, vitellogenic oocytes (diameter varied from 525 to 960 µm) had developed simultaneously (Fig. 2D). Only minor asynchrony was visible in the development of the advanced cohort of oocytes. The degree of oocyte cytoplasm filled with yolk was slightly different. However, these deviations disappeared by the completion of vitellogenesis. The zona radiata became thicker (13–17 µm), and radial striations appeared.

Females with gonads at the actively spawning subphase had a mean TL of 297.4 mm (SD 31.6), a mean BW of 1284.8 g (SD 313.2), a mean GW of 590.7 g (SD 149.3), and a mean GSI of 45% (SD 7.2). In gonads of these females, the stage of "germinal vesicle break-

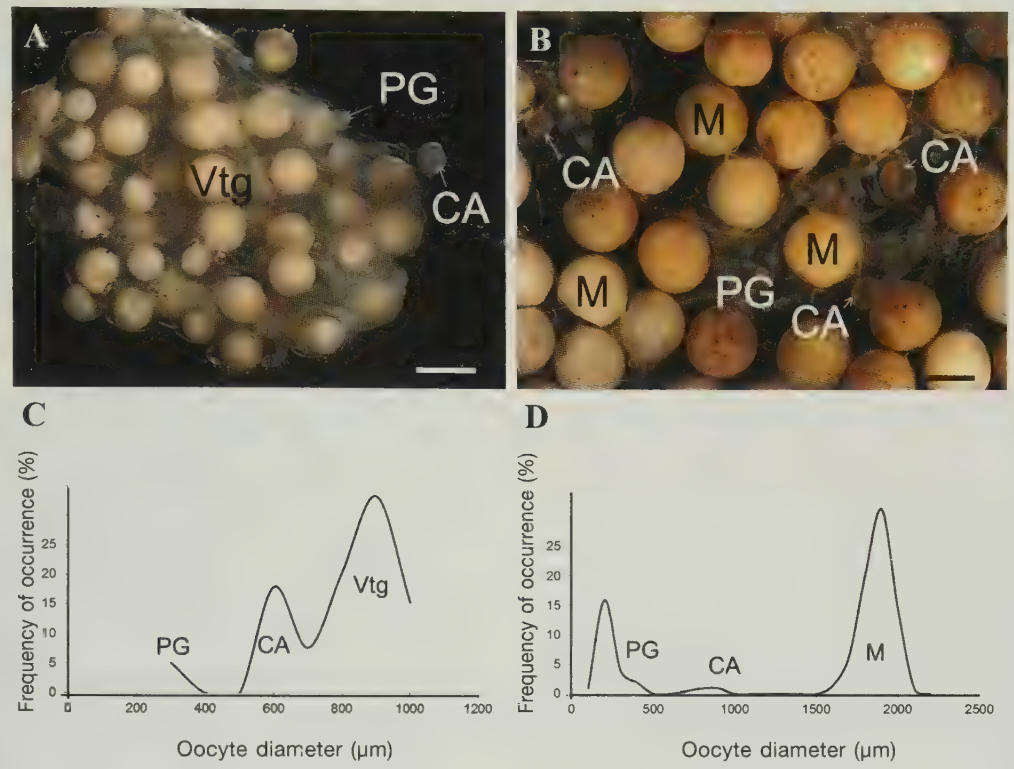

Figure 3

Photographs of the ovaries of smooth lumpsucker (*Aptocyclus ventricosus*) in the (**A**) developing phase and (**B**) actively spawning subphase and the oocyte size frequency in ovaries of the (**C**) developing phase and (**D**) actively spawning subphase. The following features are indicated: primary growth (PG); cortical alveoli (CA); vitellogenic (Vtg); and mature (M) oocytes. The length of the scale bars in the photographs represents 1 mm.

down oocytes" (Brown-Peterson et al. [2011]) with yolk homogenization was present in the ovary. The diameter of advanced oocytes increased by about 2.5 times (1401–1658 μm), and the thickness of their zona radiata ranged from 39 to 61 μm. Primary growth oocytes and oogonia, which served as the reserve fund of germ cells, occurred among mature oocytes (Fig. 2E).

Regressing and regenerating gonads were detected in 3 females, which were caught at depths of 86–138 m at distances of 26–58 nmi from the coast. The TL of these spent fish ranged between 261 and 300 mm, body weight varied between 523 and 615 g, gonadal weight varied between 32 and 64 g, and mean GSI was 7.4% (SD 4.7). Ovaries at the regressing phase were identified in 2 of these females by the presence of postovulatory follicles; primary growth oocytes were located among them. In gonads of 1 of the 3 females, we found late-stage atretic eggs, postovulatory follicles, and early primary vitellogenic oocytes that indicate a regenerating phase (Fig. 2F). No sperm were found in any of the ovaries.

The results from examination of oocyte diameters indicated group-synchronous oocyte development. In developing ovaries (Fig. 3, A and C), 3 groups of oocytes were clearly distinguishable on the basis of size. The first group was characterized by primary growth oocytes of 250-μm diameter, the second by cortical alveolus oocytes of 600-μm diameter, and the third by vitellogenic oocytes of 850-μm diameter. In actively spawning subphase gonads (Fig. 3, B and D), the majority of germ cells were in the germinal vesicle breakdown stage and ranged in diameter from 1800 to 2000 μm. There were also a reserve fund of oocytes, including primary growth and cortical alveolus oocytes of the same size as developing gonads.

Gonad maturation begins in individuals longer than 129 mm TL. Spawning and spent fish range from 218 to 300 mm TL. Therefore, mature individuals have dominated trawl catches during research surveys and commercial fishing operations in the Pacific waters off the northern Kuril Islands and southeastern Kamchatka (Orlov and Tokranov, 2008).

Our histological study on the smooth lumpsucker has shown a discontinuous type of oogenesis or determinate type of fecundity, which is characterized by 2 oocyte generations (vitellogenic oocytes and reserve fund of sex cells) in ovaries at the developing and spawning-capable phases. The reserve fund of sex cells

was represented by oogonia, primary growth oocytes, and cortical alveoli oocytes in all examined ovaries.

Values of F_{abs} ranged between 24,240 and 63,756 oocytes per female with a mean of 42,187 oocytes per female (SD10,246). The F_{rel} values ranged between 21 and 67 oocytes/g of body weight, with a mean of 36 oocytes/g of body weight (SD 9).

There was a stronger correlation between fecundity and body weight (regression equation: $y=25.187x+10{,}365$, coefficient of determination [r^2]=0.73 for F_{abs}; $y=55.454x+24{,}823$, $r^2=0.76$ for F_{rel}) than between fecundity and length ($y=194.35x-15{,}374$, $r^2=0.62$ for F_{abs}; $y=469.3x-45{,}013$, $r^2=0.65$ for F_{rel}).

Discussion

The results of our study prove that the smooth lumpsucker is an iteroparous, total spawning species according to the classifications of Murua and Saborido-Rey (2003), McBride et al. (2015), and Pavlov and Emel'yanova (2016). This reproductive strategy means that females of this species are multiple spawners and do not die after breeding, in contrast to previous opinions (Vinogradov, 1950; Fadeev, 2005). Some authors (Ilynsky and Radchenko, 1992; Orlov and Tokranov, 2008) have questioned this assertion, suggesting that a proportion of the females survive and are involved in repeated spawning. Although the scientific literature documents that a large number of dead smooth lumpsucker are found after spawning, these dead fish are actually mostly males that were protecting egg clusters (Ul'chenko and Orlov, 2001). In the closely related species of the lumpfish, females survive after spawning, exit the spawning grounds, and return offshore when oviposition is complete (Cox and Anderson, 1922; Kennedy et al., 2015). However, for the lumpfish, the results of Bagge[2] and Kasper et al. (2014) both indicate low levels of postspawning survival.

The presence of several clearly grouped oocytes in ovaries (Fig. 3) indicated discontinuous oogenesis (determinate fecundity) and group-synchronous development of vitellogenic oocytes; oocytes were released one during the spawning season (total spawning). Similar reproductive characteristics have been observed in other teleost fishes of the families Clupeidae, Cyprinidae, Salmonidae, Percidae, Scorpaenidae, and Cottidae (Muñoz et al., 2002; Petersen et al., 2004; TenBrink and Aydin[3]; McBride et al., 2015). In contrast, another member of the family Cyclopteridae, *Lethotremus awae*, is a multiple spawner during every mating season and is characterized by asynchronous development of vitellogenic oocytes (Abe and Sato, 2009) — a reproductive strategy that may be attributed to the more southern range of this species: eastern coast of central Japan and Yellow Sea near Chefoo (Pavlov and Emel'yanova, 2016).

The ovaries of the smooth lumpsucker are characterized by the absence of sperm in all gonads, indicating gonochorism, oviparity, and external fertilization (Devlin and Nagahama, 2002). The size of mature oocytes and thick zona radiata are similar to those of some members of the families Salmonidae, Pleuronectidae, Hexagrammidae, Hemitripteridae, Cottidae, and Clupeidae, which have adhesive demersal eggs that are deposited on a variety of substrates. A thick envelope protects these demersal eggs from mechanical damage during development in the coastal zone (Warfel and Merriman, 1944; Ivankov and Kurdyayeva, 1973; Stehr and Hawkes, 1979; Markevich, 2000; Kolpakov and Dolganova, 2006; TenBrink and Buckley, 2013). Oil droplets appear in the cytoplasm of chromatin nucleolar oocytes and are present until the embryonic stage (Kyûshin, 1975).

We found that smooth lumpsuckers from the Sea of Okhotsk and near the southern Kuril Islands had absolute fecundity values less than or equal to those reported elsewhere. Kyûshin (1975) reported absolute fecundity values ranging from 45,500 to 80,000 eggs for smooth lumpsucker collected in February off the Shikabe coast (Funka Bay, southern Hokkaido, Japan). Absolute fecundity values varying from 30,000 to 50,000 eggs were reported off the southeastern coast of the Kamchatka Peninsula (Vinogradov, 1950).

Our study has extended current knowledge on oogenesis, reproductive strategy, fecundity and has identified specific features of the reproduction of the smooth lumpsucker. Snailfishes (Liparidae) have some features, such as large eggs, low fecundity, the laying of eggs in sheltered locations with the use of the female ovipositor, and possibly the protection of clutches in species having a large sucking disk (Rass, 1950; Stein, 1980; Chernova, 2014), that are similar to features of the smooth lumpsucker, but members of Liparidae have not been studied in detail. The data from our study may help to elucidate the reproductive biology of this closely related group of fishes.

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Underwater video surveillance of American lobsters (*Homarus americanus*) to understand saturation levels in lobster traps

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Abstract—Estimates of abundance of the American lobster (*Homarus americanus*) are often based on catch data and are, therefore, potentially influenced by trap saturation (a plateau in catch levels over time). Although aspects of trap saturation in standard lobster traps have been investigated, less is known about the process of saturation in *ventless* traps that are currently used for stock assessments. Our goal was to investigate the possible mechanisms leading to trap saturation in ventless and standard lobster traps, by using in situ time-lapse video surveillance. The dynamics of saturation in standard traps were difficult to assess in this study because entry and escape rates were similar throughout each trial, under the conditions tested; therefore, few lobsters accumulated in the standard traps. In contrast, few lobsters escaped from ventless traps used under the same conditions. Lobsters consistently accumulated in ventless traps during the first day of fishing, and then the catch plateaued on the second day as fewer lobsters entered those traps. On the second day of soaking, catch apparently reached a dynamic equilibrium in which the rate of entry declined to the point where it was equal to the rate of escape.

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Effective monitoring is important for successful management of fish and shellfish populations, especially given the impacts of overfishing and a changing ocean climate (Brander, 2010). Catch per unit of effort (CPUE) is currently the most widely used indicator of abundance for the American lobster (*Homarus americanus*), which is the focus of one of the most valuable fisheries in the United States and Canada. Furthermore, CPUE is an important metric for stock assessments. However, owing to concerns that catch in traps may not provide an accurate index of actual populations under certain conditions (Watson and Jury, 2013), several U.S. states (Maine, New Hampshire, Rhode Island, and Massachusetts) now conduct annual surveys with ventless traps to better estimate relative abundances of American lobsters (MDMR[1]; MADMF[2]).

Determining indicators and reference points for American lobster abundance, particularly those of prerecruits, remains an ongoing challenge (Caddy, 2004; Steneck, 2006). Jury et al. (2001) showed that approximately 94% of American lobsters that entered standard traps ultimately escaped and, of those that escaped, 28% exited through the es-

[1] MDMR (Maine Department of Marine Resources). 2011. Maine Department of Marine Resources 2011–2012 research plan, 27 p. [Available from website, accessed January 2017.]

[2] MADMF (Massachusetts Division of Marine Fisheries). 2014. Massachusetts Division of Marine Fisheries 2014 annual report. [Available from website, accessed January 2017.]

Table 1

Summary of the 6 trials in which a video surveillance system attached to lobster traps was used to investigate trap saturation in ventless (3 trials) and standard traps (3 trials) deployed off New Hampshire (Wallis Sands) during 2010–2012. The total number of hours of recorded video excludes nighttime footage because the lobster-trap video system recorded behavior of American lobsters (*Homarus americanus*) only during the day (~0900–1700 or 1900 h). Density represents the number of lobsters on the bottom during each trial. The final catch values in traps were calculated on the basis of the number of entries and escapes observed in videos.

Trial	Trap type	Start date	End date	Total hours recorded	Density (individuals/m^2)	Final catch (no. of lobsters)
1	Standard	09/24/2010	09/25/2010	15.8	0.136	3
2	Standard	06/28/2011	06/29/2011	24.4	0.053	0
3	Standard	07/18/2012	07/19/2012	19.3	0.054	1
4	Ventless	09/14/2010	09/15/2010	19.5	0.136	14
5	Ventless	08/06/2011	08/07/2011	15.7	0.100	28
6	Ventless	08/25/2011	08/26/2011	15.3	0.140	27

cape vents in the parlor; the remaining 72% escaped from the kitchen, where the bait was located, through one of the 2 entrances. Although the exit of sublegal-size lobsters through the escape vent is advantageous for sustaining lobster populations, it is clear that catch in standard traps does not always correlate well with either the abundance or size composition of lobster populations on the bottom (Courchene and Stokesbury, 2011; Watson and Jury, 2013; Clark et al., 2015). Ventless traps, which lack escape vents (Estrella and Glenn[3]), help to alleviate this problem and, for this reason, are being used in assessments by some state fisheries management agencies (MADMF[2]).

Recently, Clark et al. (2015) showed that ventless traps provide a better representation of American lobster density and size composition than standard traps. Although the time it took for ventless traps to *saturate*, or reach a point where catch plateaued (16–24 h), was similar at different lobster densities surrounding the experimental traps, the maximum catch was correlated with the greatest lobster density surrounding the traps. In other words, traps saturated at a level of catch that was much less at low densities of lobsters than at higher densities; therefore, ventless traps were saturating not because they had reached a theoretical maximum capacity but for reasons that have yet to be determined. The major goal of this investigation was to use underwater video surveillance techniques to observe and quantify the behavior of American lobsters in and around ventless and standard traps in order to gain a better understanding of the mechanisms underlying trap saturation, defined as a plateau in catch over time, in both trap types.

Video surveillance makes it possible to study animals in their natural habitats without the interference of humans (Mallet and Pelletier, 2014). For example, Jury et al. (2001) attached a video recording system to a standard lobster trap and noted the behaviors of American lobsters in and around a trap for up to 48 h. The data from that study indicated that many of the lobsters that enter traps ultimately escape. Subsequently, other investigators used similar methods to observe the behavior around traps of commercially important marine crustaceans, including the Caribbean spiny lobster (*Panulirus argus*; Weiss et al., 2006), Japanese rock crab (*Charybdis japonica*; Vazquez Archdale et al., 2007), Dungeness crab (*Cancer magister*; Barber and Cobb, 2009), and blue crab (*Callinectes sapidus*; Reichmuth et al., 2011).

Despite these advances, the mechanisms that cause saturation in crustacean traps are still not fully understood. The most generally accepted explanation is that trap saturation is due, in part, to the competitive and agonistic interactions between conspecifics inside and outside a trap (Richards et al., 1983; Miller, 1990; Addison, 1995; Jury et al., 2001; Barber and Cobb, 2009; Ovegård et al., 2011). For example, pots used to catch Dungeness crab are believed to saturate because of agonistic interactions between entering crabs and approaching crabs (Barber and Cobb, 2009). Similar territoriality has been observed in and around lobster traps (Richards et al., 1983; Addison, 1995; Jury et al., 2001). Prestocking standard traps with American lobsters caused a reduction in entry rate and therefore catch (Richards et al., 1983; Addison, 1995; Watson and Jury, 2013). These findings, combined with those of Jury et al. (2001), suggest that saturation of standard traps is at least partially a function of increased agonistic interactions between lobsters in and around traps—interactions that reduce the rate of entry as traps accumulate lobsters. However, if agonistic interactions were the only cause of saturation, then traps would be expected to reach this plateau sooner at higher densities. Clark et al. (2015) observed that the catch

[3] Estrella, B. T., and R. P. Glenn. 2006. Lobster trap escape vent selectivity. Mass. Div. Mar. Fish., Tech. Rep. TR-27, 15 p. [Available at website.]

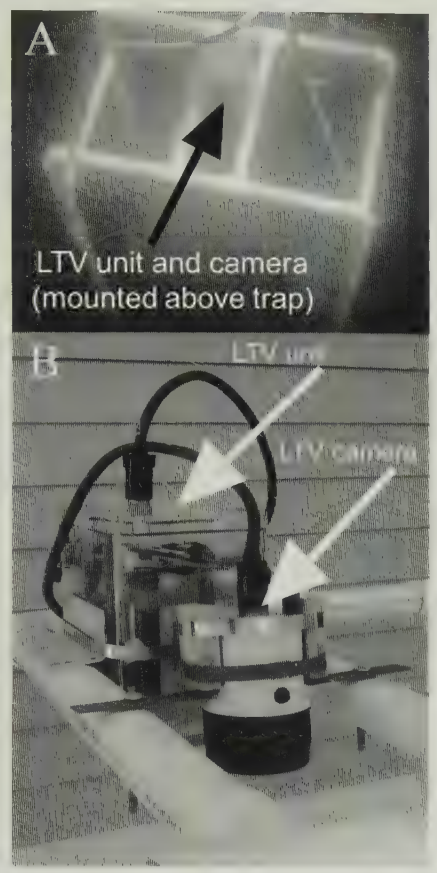

Figure 1

Photographs of the lobster-trap video (LTV) system used to investigate trap saturation in ventless and standard traps deployed off New Hampshire (Wallis Sands) during 2010–2012. **A**) View of the LTV system mounted on a standard lobster trap, placed underwater, at the study site. **B**) Close-up view of the LTV system, which includes a camera mounted in an underwater flashlight housing that was connected to another waterproof housing containing a digital video recorder (DVR) and batteries. Note that the DVR is not visible.

in lobster traps consistently plateaued after 16 to 24 h for both high and low densities of lobsters. Thus, other factors that potentially influence trap saturation in both standard and ventless traps were the focus of our study.

Our objective was to identify factors that affect the saturation of lobster traps. The behavior of American lobsters was observed by using a modification of the lobster-trap video system that had been incorporated into previous studies conducted off New Hampshire (Jury et al., 2001; Watson and Jury, 2013). We hypothesized that changes in the entry rate in relation to the escape rate over the period of a soak would cause catch in traps to plateau.

Materials and methods

Study site

All data from video surveillance of traps were collected from 2010 to 2012 at a study site (0.8×2.5 km) just offshore of Wallis Sands State Beach in Rye, New Hampshire (for details, see Clark et al., 2015). This location was chosen because previous trap studies were conducted there to take advantage of the predominantly sandy bottom, which made it easier to obtain accurate estimates of the density of American lobsters during dive surveys and to observe lobsters around the traps by using our digital video system. Additionally, few commercial lobstermen fished in this area throughout our study.

Trapping trials and dive surveys

Between June and September of 2010–2012, 6 trials (3 with standard traps and 3 with ventless traps) were completed (Table 1). During these 6 trials, the densities of American lobsters were similar, all of the traps were deployed for 2 d, and high-quality video recordings of lobster activity were obtained. Traps were baited at the beginning of each trial with 3–4 frozen Atlantic herring (*Clupea harengus*; ≥0.2 kg in total) from the same source (Little Bay Lobster Co.[4], Newington, NH).

Dive surveys (n=8) were performed a week before or after the 6 trapping trials to estimate densities of lobsters and to determine the size composition of the lobster population in the area fished with traps. The methods for the dive surveys are described in Clark et al. (2015). Briefly, 2 scuba divers swam along 4 transects (30–60 m×4–6 m, depending on visibility), one transect in each of the cardinal directions. Before trap de[ployment, lobsters were counted to estimate lobster densities. After each trial, lobsters were collected by divers to determine size composition of the lobster population. Divers handled lobsters only during the surveys that were conducted after each trial or after the traps were hauled. Handling the lobsters before trap deployment would have potentially caused lobsters to move out of the area during the trials, a change that would, thereby, have altered the density of lobsters. The data from these surveys were converted to density estimates, as the number of individuals per square meter, for analyses. For the lobsters that were brought to the surface, carapace length (CL) and sex were recorded before the lobsters were returned to their area of capture. The mean CL of the lobsters measured during the dive surveys was 46.4 mm (standard error of

[4] The mention of trade names or commercial products throughout this article is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

Figure 2

A single frame of video recorded with a lobster-trap video system attached to a standard lobster trap deployed off New Hampshire (Wallis Sands) in 2011. Note that the cover of the trap has been replaced with a plexiglass cover so that the features of the trap (kitchen, parlor, entrance heads, escape vent) and the American lobsters (*Homarus americanus*) inside the trap can be observed more readily. Unlike the ventless trap used in this study, the standard trap contained an escape vent.

the mean [SE] 1.27), and values ranged from 25 to 160 mm. Lobsters caught during the 6 trials in ventless traps had a mean CL of 60.2 mm (SE 1.14) and, of these lobsters, less than 1% were at or above the lower legal-size limit for the American lobster inshore fishery (83 mm CL). None exceeded the upper legal-size limit for the fishery (127 mm CL).

The 6 trials included in this study were conducted at a mean lobster density of 0.1 individuals/m^2 (SE 0.02; n=8), which was consistent between trials and relatively high for this area and season (June to September; Clark et al., 2015). The mean water temperature across the trials was 16.1°C (SE 1.2).

Trap video system

The video system used in this study, lobster-trap video system (LTV), was modified from the original system developed by Jury et al. (2001). A fisheye bullet camera with a charge-coupled device chipset, 0.5 lux low light sensitivity, and 2.2-mm wide-view lens (Model PC221-HR, Sony Corp., Tokyo, Japan) was sealed inside an underwater flashlight case and mounted on the top of a PVC frame (Fig. 1A), 122 cm above the trap. The camera was connected by a waterproof cable to a water-tight acrylic case containing a mini digital video recorder (DVR) with a resolution of 640×480 lines (Model UV-K206, Unique Vision Technology Co., Ltd., Shenzhen, China) and encasing several 12V batteries (Fig. 1B). The DVR was programmed to capture videos at a rate of 5 frames/s and was turned on at dawn and off at dusk with a digital timer to save power. Only footage collected during the daylight hours of day 1 and day 2 was included in the analyses. No data were obtained at night because rate of trap entry does not generally differ between day and night at this location (Jury et al., 2001), and the addition of lights could have influenced American lobster behaviors. Digital recordings were stored on a Secure Digital High Capacity memory card (16 GB) and transferred to a computer for analyses after each trial. The replacement of the trap lid with transparent plexiglass made it possible for viewers of video recordings to more readily observe lobsters inside of the kitchen and parlor areas of traps (Fig. 2). Digital videos were obtained for a duration of 6.7 h (SE 1.1) on day 1 and 9.0 h (SE 1.6) on day 2 (Table 1).

The dimensions of each standard and ventless trap are provided in Clark et al. (2015). Briefly, the wire

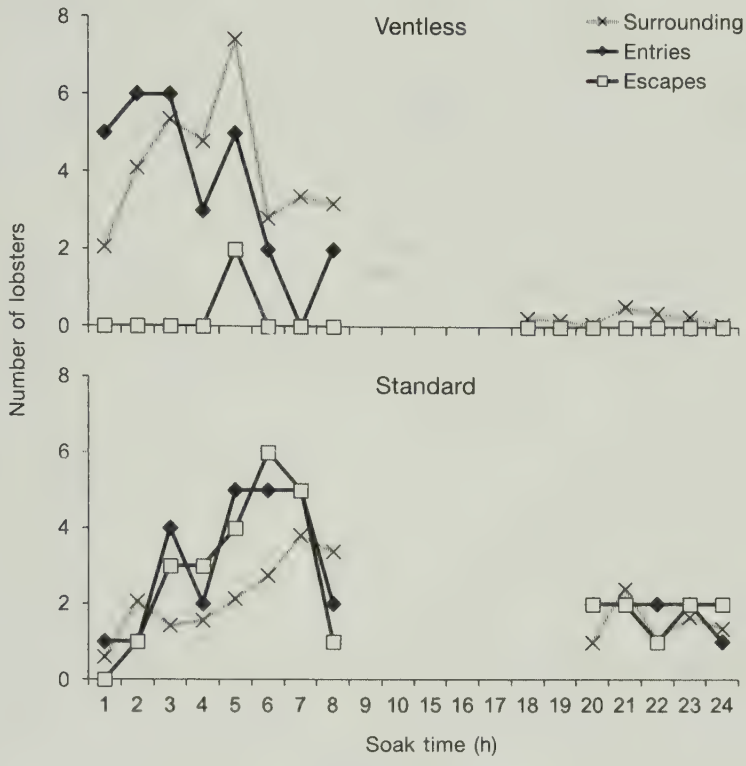

Figure 3

Number of American lobsters (*Homarus americanus*) observed surrounding, entering, and escaping a ventless trap per hour and recorded by video during a single representative trial on day 1 (hours 1–8) and day 2 (hours 18–24) off New Hampshire (Wallis Sands) in 2011. Similar data are presented for a standard trap on day 1 (hours 1–8) and day 2 (hours 20–24). Data are missing between days because the lobster-trap video system was turned off at night.

mesh for all traps was 2.5×2.5 cm and the rectangular trap dimensions were 90×47×35 cm. The kitchen of each trap contained 2 entrances, both 12.7 cm in diameter (Fig. 2). The parlor of each standard trap had a single escape vent (14.6×4.9 cm); ventless traps had no escape vents.

Data analysis

To determine factors that influenced trap saturation, the following parameters were quantified for each hour of observation of video recordings: 1) the number of American lobsters entering, escaping, and surrounding the traps and 2) the accumulated catch. When lobsters entered the trap, they continued to be observed to determine whether they would enter the parlor or leave the trap (see Fig. 2). In general, lobsters could not be identified individually; therefore, if a lobster left the field of view and then returned, it was treated as a new lobster. The rates at which lobsters accumulated in traps were calculated by using linear regression analyses. The statistical analyses presented here were performed with RStudio, vers. 1.0.136 (RStudio Team, 2009). Because videos were not recorded at night, the beginning of saturation for ventless traps (between 16 and 24 h; Clark et al., 2015) was not captured; therefore, segmented linear regression analyses were used to estimate rates of accumulated entries, escapes, and catch. Each parameter (total number of lobsters entering, escaping, and surrounding traps) was compared by using a Mann-Whitney *U* test. Only the first 3 h of footage recorded on day 1 and on day 2 were incorporated into the analyses because these recordings had the highest quality across all trials. For example, the total number of lobsters entering all ventless traps (n=3) within the first 3 h on day 1 was compared with the total number of lobsters entering within the first 3 h on day 2. To compare CPUE in standard and ventless traps, catch values were first transformed by using the natural log and then analyzed by using the Mann-Whitney *U* test. All reported variations are standard deviations (SD) unless indicated otherwise.

Table 2

Mean number of American lobsters entering, escaping, and surrounding each trap per hour during 6 trials in which ventless and standard traps were deployed for periods of 2 d off New Hampshire (Wallis Sands) during 2010–2012. The means and standard deviations (SD) were calculated by using data from the first 3 h of each day.

		Number of entries (SD)		Number of escapes (SD)		Number of lobsters surrounding traps (SD)	
Trial	Trap type	Day 1	Day 2	Day 1	Day 2	Day 1	Day 2
1	Standard	4.7 (2.1)	0	4.0 (2.0)	0	3.4 (1.9)	3.1 (0.2)
2	Standard	3.7 (2.9)	4.0 (1.0)	4.0 (3.6)	3.3 (2.1)	2.5 (0.8)	1.6 (0.1)
3	Standard	2.0 (1.7)	2.0	1.3 (1.5)	1.7 (0.6)	1.4 (0.7)	1.5 (0.8)
4	Ventless	2.7 (0.6)	0.3 (0.6)	1.0 (1.7)	0	2.2 (0.6)	0.3 (0.1)
5	Ventless	5.7 (3.1)	1.3 (1.2)	1.0 (1.7)	0.7 (0.6)	3.5 (0.1)	0.6 (0.4)
6	Ventless	5.7 (0.6)	0	0	0	3.8 (1.7)	0.2 (0.1)

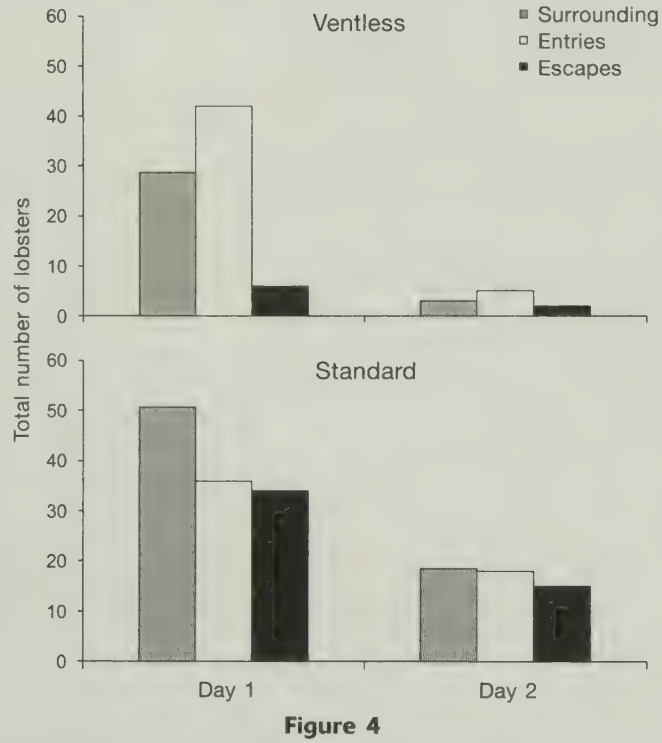

Figure 4

Number of American lobsters (*Homarus americanus*) observed surrounding, entering, and escaping ventless traps (n=3) and standard traps (n=3) over the first 3-h period of video footage recorded on day 1 and day 2 of deployments off New Hampshire (Wallis Sands) during 2010–2012.

To determine whether American lobsters inside the trap inhibited the entry of approaching lobsters, *half-entries*, defined as any instance in which a lobster made contact with the mesh funnel of the kitchen entrance but did not fully enter the kitchen (Jury et al., 2001), were quantified. Our working hypothesis was that if the lobsters inside the trap inhibited other lobsters from entering the trap on day 2, the number of half-entries should be higher on day 2 than on day 1. Because we expected more lobsters to have accumulated inside the ventless traps by day 2, we also expected more agonistic interactions between entering lobsters and the lobsters already in the trap and, therefore, more half-entries toward the end of each trial. After calculating the total number of half-entries, we used the Mann-Whitney U test to determine whether differences existed over time and between trap types.

Results

Movements in, and around, standard and ventless traps

A similar number of American lobsters entered ventless traps and standard traps on day 1 (Figs. 3 and 4, Table 2; Mann-Whitney U=7, P>0.05). There was also no significant difference in the number of lobsters surrounding each trap (Mann-Whitney U=7, P>0.05). However, significantly more lobsters escaped from standard traps than from ventless traps (Mann-Whitney U=0, P<0.05). On day 2, a similar number of lobsters entered (Mann-Whitney U=2.5, P>0.05) and escaped (Mann-Whitney U=2, P>0.05) each respective trap type. For example, on day 2, 5 lobsters entered ventless traps and 2 escaped. Even so, there were fewer lobsters surrounding ventless traps than standard traps (Mann-Whitney U=0, P<0.05).

Fewer lobsters entered ventless traps on day 2 than on day 1 (Figs. 3 and 4, Table 2; Mann-Whitney U=9, P<0.05). Although there was no difference in the number of lobsters escaping from ventless traps on day 1 versus day 2 (Mann-Whitney U=7, P>0.05), significantly fewer lobsters surrounded the ventless traps on day 2 than on day 1 (Mann-Whitney U=9, P<0.05).

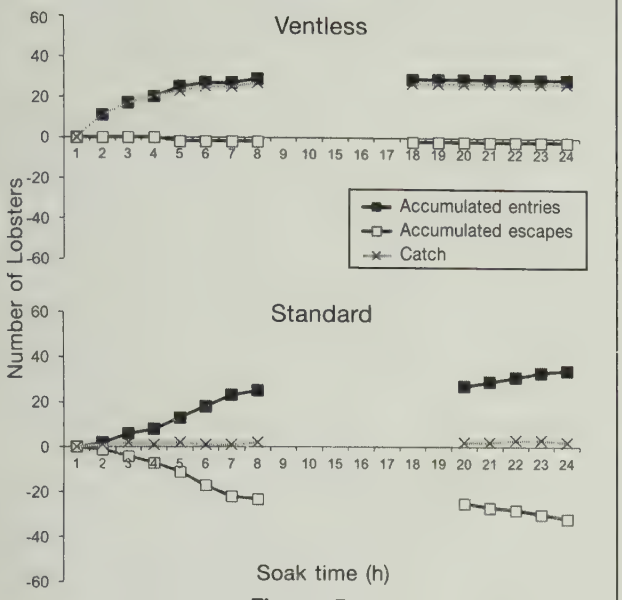

Figure 5

Number of entries, escapes, and catch of American lobsters (*Homarus americanus*) accumulated per hour during a single representative trial with a ventless trap and a single trial with a standard trap over 8 h on day 1 and 5–7 h on day 2 (no data were collected at night). Both traps were deployed off New Hampshire (Wallis Sands) during 2010–2012.

For standard traps, approximately the same number of lobsters entered (Mann-Whitney U=6.5, P>0.05), escaped (Mann-Whitney U=7, P>0.05), and surrounded the traps (Mann-Whitney U=5, P>0.05) throughout the 2-d soak.

Accumulated entries and escapes

Some trap dynamics differed between day 1 and day 2. For ventless traps, the rates of entry, escape, and catch on day 1 exceeded those observed on day 2 (Figs. 5 and 6; Mann-Whitney U=9, P<0.05 for all variables). For standard traps, the rates of entry, escape, and catch did not significantly differ over the 2-d soak (Mann-Whitney U=7, P>0.05). Because entry rate and exit rate were equivalent on each day, standard traps caught lobsters at similarly low rates on days 1 and 2 (Mann-Whitney U=6, P>0.05); therefore, very few, if any, lobsters were captured by the standard traps. In contrast, ventless traps had higher CPUE on day 1 than on day 2 (Mann-Whitney U=9, P<0.05). The lobsters could not easily leave the ventless traps because of the absence of an escape vent and, as a result, escape rates were lower than entry rates on day 1 (~1 individual/h in contrast with 7 individuals/h, respectively). Ventless traps continued to accumulate lobsters until catch plateaued on day 2 (Fig. 5). At the end of each trial, ventless traps had higher CPUE than standard traps (Fig. 7; Mann-Whitney U=9, P<0.05).

Comparison of half-entries on days 1 and 2 of the soak period

A similar number of half-entries took place in the 2 types of traps on day 1 (Fig. 7; Mann-Whitney U=5, P>0.05) and on day 2 (Mann-Whitney U=4.5, P>0.05). Moreover, there was a higher frequency of half-entries on day 1 than on day 2 for standard and ventless traps (Mann-Whitney U=9, P<0.05).

While quantifying half-entries, we identified the following types of deterrents to entrapping American lobsters: 1) disturbance of entering lobsters by approaching conspecifics; 2) agonistic interactions of approaching lobsters with lobsters that were already inside the trap; 3) current-induced movements of the bait bag that potentially startled lobsters; and 4) apparent loss of interest of approaching lobsters (cause *unknown*). Deterrents for half-entries were classified as unknown if a lobster approached the trap, usually making contact with it, but left without any obvious cause. Unlike lobsters that exhibited a half-entry for one of the reasons listed above, the lobsters that half-entered for no apparent reason rarely exhibited an avoidance response (i.e., tail-flipping) before leaving the field of view. In both types of traps, half-entries occurred predominantly because of either loss of interest (unknown) or intimidation by approaching lobsters. Loss of interest was responsible for 43% and 55% of the half-entries observed in ventless and standard traps, respectively, and intimidation by approaching lobsters accounted for almost 30% of the half-entries in each trap type. Agonistic interactions with lobsters inside of ventless and standard traps were responsible for 18% and 11% of the half-entries, respectively. The movement of bait bags within each trap had the least effect, causing <10% of the half-entries.

Discussion

The results from this set of experiments provide insight into the mechanisms that are likely responsible for the saturation of lobster traps, particularly ventless traps. For example, catch of American lobsters in ventless traps reached a plateau on day 2 of a soak owing, in part, to a reduction in the rate at which lobsters entered the traps. The data illustrated in Figures 3 and 5 indicate that this leveling off of entry rate may be due, at least partly, to a decrease in the density of lobsters in the vicinity of the trap. This decrease in the number of lobsters surrounding traps may have occurred because ventless traps accumulated so many lobsters that they effectively reduced the local density of lobsters. However, in a more recent study (W. Watson, unpubl. data), the results of dive surveys that corresponded with trap trials indicate that the number of lobsters in the fishable area did not change between day 1 and day 2; therefore, we hypothesize that other factors, such as loss of bait attractiveness after approximately 24 h, may be the reason that fewer lobsters approached and entered both types of traps on day 2 versus day 1.

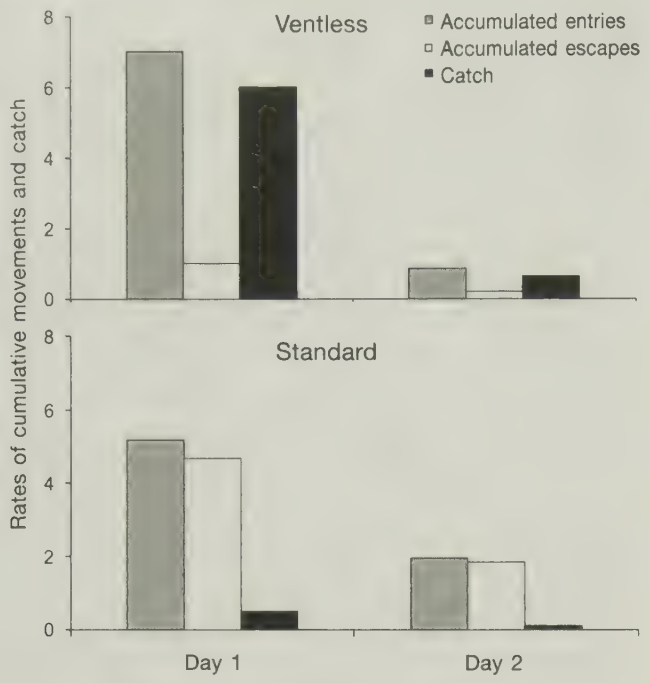

Figure 6

Rates at which entries, escapes, and catch of American lobsters (*Homarus americanus*) accumulated in ventless traps (n=3) and standard traps (n=3) over the first 3-h period on day 1 and day 2 of deployments off New Hampshire (Wallis Sands) during 2010–2012. Rates were calculated by using the slopes of the regression lines fitted to each segment of data points.

Agonistic encounters

Behavioral interactions between American lobsters and their conspecifics in proximity of the traps are closely linked to a reduction in overall trap catch (Richards et al., 1983; Miller, 1990; Frusher and Hoenig, 2001; Barber and Cobb, 2009). Similar interactions were observed in our study. Many experiments have confirmed that American lobsters are aggressive in their inter- and intraspecific interactions (Tamm and Cobb, 1978; Rutishauser et al., 2004; Steneck, 2006; Williams et al., 2006; Williams et al., 2009); therefore, agonistic behavior is common among American lobsters congregating in and near lobster traps (Jury et al., 2001), as is the case with other decapods, including the rock lobster (*Jasus edwardsii*; Ihde et al., 2006), and the giant mud crab (*Scylla serrata*; Robertson, 1989), and the European green crab (*Carcinus maenas*; Bergshoeff et al., 2018). In all of these studies, agonistic encounters contributed to reduced trap entry, a factor believed to cause trap saturation (Miller, 1979).

"Prestocking" traps with lobsters is one way to determine whether lobsters inside traps reduce catch of their conspecifics. Richards et al. (1983) showed that prestocking traps inhibits the catch of additional lobsters and some crab species (e.g., *Cancer* spp.). A more recent study has provided evidence that prestocking reduces the rate of entry, but it does not reduce the total catch in standard traps if the total catch includes the stocked lobsters (Watson and Jury, 2013). However, it should also be noted that, in general, traps in most of the previous studies were stocked with adult, legal-size lobsters, but in this study, many of the lobsters observed in and around the traps were of sublegal size. Interestingly, in our study, interactions with lobsters inside the traps did not appear to be the dominant cause of half-entries. Rather, disturbance by lobsters outside of the traps accounted for almost 30% of half-entries for each trap type. When the lobsters approached the traps, other encroaching lobsters outside of the traps often deterred their conspecifics from entering by lunging at them or chasing them away from the trap entrances. This type of behavior was observed around both standard and ventless traps and limited the frequency of successful entries into each trap type. Even when there were lobsters inside the kitchen, entry rates were influenced more by interactions outside of the traps and, therefore, by the density of lobsters around the traps.

Most lobsters in ventless traps accumulated in the parlor area of traps, rather than the kitchen, and it is unlikely that they directly influenced subsequent trap entries unless there were other deterrent cues provided by trapped lobsters (e.g., olfactory cues, auditory cues). Importantly, with regard to the mechanisms that lead to catch leveling off at some value, there were fewer half-entries on day 2, for both trap types, than on day 1 (Fig. 7); therefore, agonistic interactions between lobsters inside and outside of the traps may have contributed to the reduction in trap entries, as observed in previous studies, but they were likely not the reason entries and catch leveled off on day 2.

The decline in lobsters outside of the ventless traps on day 1 was negatively correlated with the number of lobsters inside the traps. However, because the lobsters were not tagged, it was not possible to track the movement of individuals; therefore, we cannot conclude that lobsters in the surrounding field of view at the point of trap deployment were, in fact, the same lobsters that were caught later in the trial. Nonetheless, the relationship between increasing catch by ventless traps and decreasing number of surrounding lobsters (observed) indicates that these lobsters are partially removed from the fishable area of the trap. On the other hand, the number of lobsters that surrounded standard traps did not significantly differ between day 1 and day 2. This difference between trap types may have been a result of the size-frequency distribution of lobsters in this area—a distribution over which most of the lobsters (>99%) were below legal size (as determined by using data from dive surveys). Because of their size, many lobsters were able to exit through the

escape vents in standard traps (Nulk, 1978; Saila et al., 2002; Courchene and Stokesbury, 2011), and some of them likely remained in the vicinity of the traps.

Entry and escape rates

The rate of American lobster entries and escapes varied between the 2 types of traps. For standard traps, lobsters entered and escaped at approximately the same rates each day (Figs. 5 and 6), resulting in an overall low catch when traps were hauled on day 2. In standard traps, when a lobster entered through the kitchen entrance, it would either escape through the entrance or move into the parlor (Fig. 2). As observed by Karnofsky and Price (1989), lobsters often escaped the parlor shortly after entering it (<2 min). Similarly, in our study, standard traps did not saturate because, once a lobster entered the trap, that same lobster, or one of the other lobsters already in the trap, left shortly thereafter.

Ventless traps filled with lobsters at a rate of ~7 individuals/h on day 1, but the rate of entry by day 2 slowed to about 12% of the rate of day 1. Because very few lobsters escaped from the ventless traps, a relatively high number of lobsters accumulated in ventless traps on day 1 and an average of 23 individuals (SD 7.8) remained in the trap until the end of the 2-d soak (Table 1, Figs. 5–7). The mean density of lobsters during trap deployment was 0.1 individuals/m^2 (SD 0.02). Assuming that a typical effective fishing area around a trap is deployed for a 24-h soak is 2600 m^2 (Watson et al., 2009), there would be a pool of 260 lobsters (0.1 individuals/m^2×2600 m^2) that might approach or encounter a trap in day 1. Fewer than 260 lobsters approached the ventless trap in each trial of this study; therefore, it is unlikely that ventless traps saturated from catching all of the available lobsters. Our data do not support the hypothesis that depletion, or reduction, in the number of lobsters within the effective fishing area is a primary cause of trap saturation.

Approximately 40–50% of the bait, determined by weight, remained in ventless traps after having soaked for 24–48 h (Clark, 2012). Interestingly, ventless traps retained more bait by weight than standard traps after 48 h, possibly because lobsters repeatedly escaped and re-entered the standard traps to consume the remaining bait (Clark, 2012; Clark et al., 2015). However, even though bait remained, the olfactory attractiveness of the bait likely declined after a 24-h soak, as a result of the leaching of attractants (W. Watson, unpubl. data). We hypothesize that because typical lobster bait releases more odorants early in the soak time (i.e., <24 h), the rate of entry into traps eventually declines and an equilibrium between entries and escapes is reached, leading to a plateau in catch level and trap saturation.

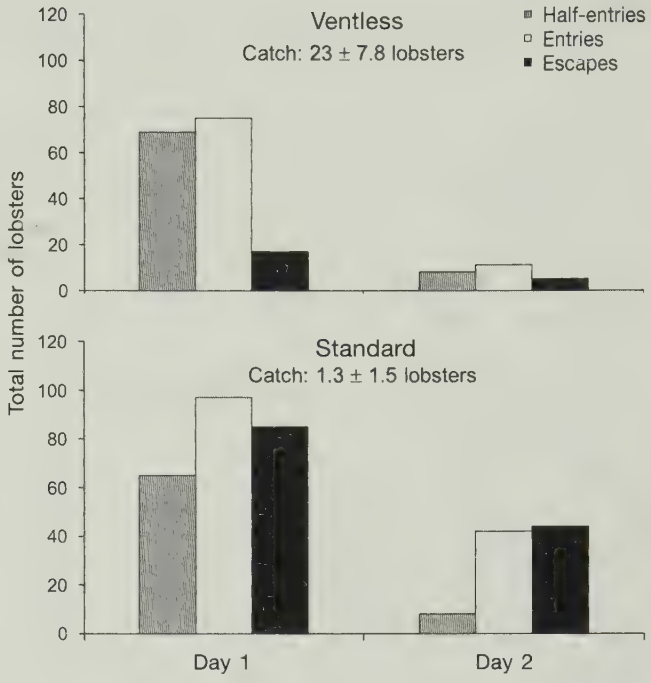

Figure 7

Number of half-entries, entries, and escapes of American lobsters (*Homarus americanus*) in ventless traps (n=3) and standard traps (n=3) during the first 3-h period on day 1 and day 2 of deployments off New Hampshire (Wallis Sands) during 2010–2012. Catch values represent the mean number of lobsters caught in ventless traps and standard traps after each trial, determined by cumulative number of entries and escapes (Table 1, Fig. 6). A half-entry is an instance when a lobster makes contact with the mesh funnel of a kitchen entrance in a trap but does not fully enter the kitchen.

Acknowledgments

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Adaptive and plastic variation in growth and maturation of the cutlassfish *Trichiurus japonicus* in the subtropical Pacific Ocean

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Abstract—We investigated variation in growth and maturation in response to 1) spatial variation in climate and 2) exploitation of the subtropical cutlassfish *Trichiurus japonicus*, an important fishery species whose population ecology is virtually unknown. Individuals of this cutlassfish species were sampled monthly at 2 primary landing sites: Kengfang, in northeast (NE) Taiwan, and Tsukuan, in southwest (SW) Taiwan, during 2013–2015. Habitat temperatures were about 1–4°C lower at the NE site than at the SW site, and the length at age of adult fish had an inverse pattern with temperature (NE lengths >SW lengths at age). The probabilistic maturation reaction norms did not differ significantly between the 2 areas, but ages and lengths at maturation were higher for males from NE than for males from SW. Differences in asymptotic lengths (NE>SW) and growth coefficients (NE<SW), together with narrower length distribution at the SW site than at the NE site, indicate potentially different mortality between the areas (NE<SW). These results indicate plastic variation in maturation and potentially adaptive variation in growth for this species that are related to the differences in temperature and mortality between the areas, although reliable proxies for mortality are lacking. The observed life-history variation was consistent with the temperature–size rule that organisms tend to grow faster, mature earlier, and reach smaller asymptotic sizes at warmer temperatures and may indicate an adaptive divergence of cutlassfish populations.

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Life-history traits (i.e., growth rate, and age and length at maturation) are key determinants of population demography and the rates of population growth (Roff, 1992; Stearns, 1992) and provide insight into the sustainability of exploited species experiencing environmental changes and fisheries exploitation (Clark, 1991; Zhou et al., 2012; Wang et al., 2014). Studies on the variation in life histories have, however, paid more attention to temperate fish species (i.e., primarily the species in the Northern Atlantic) than to subtropical or tropical species, the abundance of which is predicted to decrease significantly under the effects of climate change (Cheung et al., 2010). Consequently, it is imperative that we enhance our understanding of life-history variation for subtropical and tropical species.

Intraspecific variation in growth and maturation reflects the effects of both the physical and biological environments through a combination of phenotypic plasticity and genetic variability (Stearns, 1992; Law, 2000). For example, food availability and temperature can influence consumption and assimilation, in turn influencing an animal's energetic condition, growth rates, and maturation schedules (Saborido-Rey and Kjesbu[1]). Simultaneously, because of the heritability of life-history traits and their association with fitness attributes (i.e., fecundity and survival), physical or biological factors can potentially influence growth and maturation through adaptive processes (known as the "habitat template theory") (Southwood, 1977; Reznick et al., 1990; Arendt and Wilson, 1999). Furthermore, fishing-induced mortality also can cause plastic changes (e.g., through relaxing density-dependent processes) and adaptive genetic changes (through altering the genetic makeup of life-history traits) in growth and maturation (Law, 2000; Reznick and Ghalambor, 2005). Together, these factors can affect variation in growth and maturation for an exploited species (Carlson et al., 2007; Sharpe and Hendry, 2009; Enberg et al., 2012).

[1] Saborido-Rey, F., and O. S. Kjesbu. 2005. Growth and maturation dynamics, 26 p. [Available from website.]

A commonly observed macroscale relationship between growth and maturation with respect to variability in temperature, known as the "temperature–size rule," is that organisms tend to grow faster, mature earlier, and reach smaller asymptotic sizes at warmer temperatures than at cooler temperatures (Atkinson, 1994; Arendt, 2011; examples for fishes: Brunel and Dickey-Collas, 2010; Matta et al., 2016). Previous research indicates that this relationship may be due to the effect of temperature on asymptotic body sizes (e.g., a greater body size at cooler temperatures), which gives rise to adaptive changes in energy allocation to reproduction and other competing needs (Berrigan and Charnov, 1994; Atkinson, 1996; Angilletta et al., 2004; Hosono, 2011). Alternatively, nonadaptive temperature effects on metabolic rates may generate the same result (e.g., Angilletta et al., 2004; Munch and Salinas, 2009).

Theoretical models and concepts, such as the reaction norm model of maturation (Stearns and Koella, 1986; Stearns, 1992), provide mechanisms for the exploration of the plastic and adaptive processes of life-history traits. By definition, the maturation reaction norms represent genetically coded traits, the changes of which are evolutionarily "optimized" through changes in mortality and growth rates (Stearns and Koella, 1986; Stearns, 1992). The probabilistic maturation reaction norm (PMRN) approach (Heino et al., 2002; Dieckmann and Heino, 2007; Heino and Dieckmann, 2008) builds on the deterministic concept of maturation reaction norms by Stearns and Koella (1986). The PMRN approach involves statistically accounting for the major sources of plastic effects due to growth and survival and quantifying the remaining variation in maturation as more likely to represent adaptive genetic variation (Heino et al., 2002). Although this approach also is criticized (e.g., Kraak, 2007), several authors have applied this method to infer potential evolutionary changes in maturation for exploited fish species (e.g., Atlantic cod [*Gadus morhua*], Olsen et al., 2005; smallmouth bass [*Micropterus dolomieu*], Dunlop et al., 2005; and lake whitefish [*Coregonus clupeaformis*], Wang et al., 2008; reviewed by Heino et al., 2015). Furthermore, a few studies have attempted to account for other sources of plastic effects in the PMRN model, such as body condition (Grift et al., 2007; Uusi-Heikkilä et al., 2011) and social cue (e.g., presence of fish of same or opposite sex; Díaz Pauli and Heino, 2013).

Cutlassfish (some of which are also known as hairtails), including several *Trichiurus* species, are an important fisheries resource in the subtropical West Pacific (He et al., 2014; Wang et al., 2017). However, reliable species identification is difficult without the use of genetic methods, and in the FAO fisheries "capture production statistics," the catches of multiple cutlassfish species are lumped into a value for one nominal species, *Trichiurus lepturus* (Hsu et al., 2009; FAO, 2014). For this reason, and because of the lack of fishery stock assessments and regular surveys, the population ecology of individual *Trichiurus* species is poorly known. Nonetheless, *T. japonicus* is likely a dominant species that contributes substantially to the coastal catch in this region (i.e., this species accounts for 40–100% of the total cutlassfish catch; Wang et al., 2017). Also, this cutlassfish is an important predatory fish in the subtropical Pacific and, moreover, has a year-round spawning behavior (Liu et al., 2009; Shih et al., 2011).

In this study, we focused on investigating growth and maturation patterns for *T. japonicus* along the Taiwan coast in the northwestern Pacific (Fig. 1). In Taiwan, 2 primary fishing grounds are located along the northeast (NE) and southwest (SW) coasts, and together they account for about 30% (range: 24–40%) of total annual catch of cutlassfish (based on 2003–2014 data from the Taiwan Fisheries Agency[2]). The results of a previous study indicate that these fishing grounds may represent distinct populations of *T. japonicus* (Tzeng et al., 2016). In addition, environmental and fishing conditions vary between these fishing grounds. Temperatures are lower along the NE coast than along the SW coast, in particular in winter. For example, the sea-surface temperatures (SSTs) are 19.2–24.6°C in winter (December–February) and 26.3–29.1°C in summer along the NE coast (June–August), and SSTs are 22.5–24.9°C in winter and 29.0–30.4°C in summer along the SW coast (Fig. 1) (also see Jan et al., 2002). The primary fisheries on both fishing grounds are pursued by using pair trawlers, but because of a lack of stock assessments, the fishing intensity is unknown. However, the number and size of trawlers were greater on the SW coast (282 boats, primary boat size of 50–100 metric tons) than along the NE coast (232 boats, primary boat size of 20–50 metric tons; Taiwan Fisheries Agency[3]), and therefore there is a higher exploitation pressure in the SW than on the NE coast. We hypothesize that the habitat or fisheries conditions have led to faster growth rates and earlier maturation patterns of *T. japonicus* along the SW coast than along NE coast.

Our objective was to describe growth and maturation of *T. japonicus* for the 2 fishing grounds and to infer potential adaptive-versus-plastic variation in the life-history traits of this species. Because the populations of *T. japonicus* at these 2 fishing grounds likely are distinct (Tzeng et al., 2016), some variation in adaptive traits for these populations may arise as a consequence of their genetic variability. We estimated the PMRNs to evaluate potential adaptive variation in maturation schedules and explored plastic changes in maturation schedules that are due to variations in growth. Also, we explored the covariation between growth and maturation in relation to habitat differences of the two areas.

[2] Taiwan Fisheries Agency. 2015. Fisheries statistical yearbook: Taiwan, Kinmen and Matsu area 2014. Fish. Agency, Counc. Agric., Executive Yuan, Taiwan. [Available from website.]

[3] Taiwan Fisheries Agency. 2016. Fisheries statistical yearbook: Taiwan, Kinmen and Matsu area 2015. Fish. Agency, Counc. Agric., Executive Yuan, Taiwan. [Available from website.]

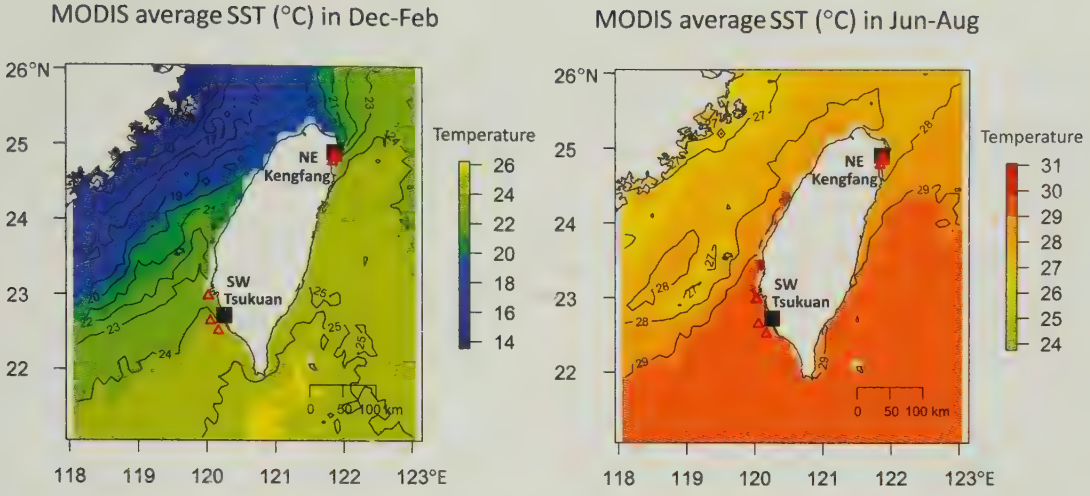

Figure 1

Map showing locations of the ports Kengfang and Tsukuan (black squares) in Taiwan where catch of the cutlassfish *Trichiurus japonicus* was sampled during 2013–2015 and locations of areas fished by the boats based at the 2 ports (open red triangles), with average summer (June–August) and winter (December–February) sea-surface temperatures (SSTs in °C) around Taiwan. The SSTs are based on Moderate-resolution Imaging Spectroradiometer (MODIS) monthly mean SSTs for 2003–2014 (NASA Goddard Space Flight Center, Sea-viewing Wide Field-of-view Sensor [SeaWiFS] Ocean Color Data, website).

Materials and methods

Sampling

We collected immature and adult cutlassfish, including the *T. japonicus*, from the pair-trawler fisheries monthly at 2 fishing ports during 2013–2015: Kengfang (also transliterated as Gengfang) on the NE coast and Tsukuan (or Ziguan) on the SW coast of Taiwan (Fig. 1). The size of fishing boats (about 40 metric tons) and the fishing methods were similar during our sampling in these areas; for example, the nets had an array of mesh sizes descending from the opening to the codend (minimum mesh size: 2.0–2.5 cm), and the fishing depths were 100–150 m on the NE coast and 100–200 m on the SW coast (senior author, unpubl. data). The trawlers operate year-round along both coasts. However, fishing seasons for cutlassfishes varied: the fisheries along the NE coast catch cutlassfishes year-round, and the fisheries along the SW coast catch cutlassfishes mainly during autumn and early spring (September–February) and catch less in other months. Despite the differences in monthly distribution of catch between the areas, we attempted to collect samples evenly across months in both areas (Suppl. Table 1) (online only). Using a stratified random sampling design, we classified fish into 5 size categories based on body depth (defined as the vertical distance between the dorsal margin of the body and the anus, in millimeters): mini (<20 mm), small (20–25 mm), medium (25–45 mm), large (45–70 mm), and extra large (>70 mm). For each sampling trip, we randomly collected 10–20 fish for each of the small, medium, and large size categories. Fish small or large enough to fall in the mini and extra-large categories were rarely found in the catch; however, we collected these animals when they were available.

Despite the use of a standardized sampling scheme, maximum lengths and length distributions of samples of *T. japonicus* varied between the 2 areas. Maximum pre-anal lengths (i.e., the distance between the tip of upper jaw and the anterior side of anus) were 752 and 379 mm for the *T. japonicus* landed in Kengfang (NE) and Tsukuan (SW), respectively (Fig. 2). Also, mean pre-anal lengths were generally smaller in Tsukuan than in Kengfang in each year and all 3 years combined (Suppl. Table 2) (online only). Distributions of sample lengths were right-skewed in Kengfang but were approximately normal in Tsukuan (Fig. 2). We conducted additional sampling in Tsukuan to obtain large *T. japonicus* specimens, but we could not find comparable samples. Therefore, the differences in length distributions between areas probably were real and not due to sampling bias.

Because of the presence of multiple cutlassfish species in the catch of trawlers, we identified the species that composed each sample on the basis of genetic analysis; the detailed methods and results of this analysis have been published in Wang et al. (2017). For the subsequent analysis described here, we used only the specimens confirmed to be *T. japonicus*.

Biological measurements

We measured total length, pre-anal length, body depth, total weight, gonad weight, sex, and maturity state for individual fish. Because tail loss was common among the sampled fish, we used pre-anal length data to conduct the analysis. We determined sex and maturity

Table 1

Sex-specific parameters—the asymptotic length (L_∞) and the Brody growth coefficient (K) derived from the von Bertalanffy growth model (Eq. 1), the counterpart parameters, $L_{\infty,inv}$ and K_{inv}, derived from the inverse von Bertalanffy growth model (Eq. 2), and minimum length (L_{min}) and daily ages (T_{min}) of cutlassfish (*Trichiurus japonicus*). Samples were collected at 2 fishing ports, Kengfang and Tsukuan on the northeast and southwest coast of Taiwan, respectively, during 2013–2015. The 95% confidence intervals are given in parentheses.

Area	Sex	L_∞ (mm)	K (per year)	$L_{\infty,inv}$ (mm)	K_{inv} (per year)	L_{min} (mm)	T_{min} (d)
Kengfang (NE)							
	Male	370 (304–436)	0.32 (0.22–0.42)	576 (411–1275)	0.17 (0.07–0.28)	48	34
	Female	520 (407–633)	0.21 (0.15–0.27)	1094 (659–3068)	0.08 (0.03–0.15)	–	–
Tsukuan (SW)							
	Male	264 (238–290)	0.56 (0.42–0.70)	399 (337–488)	0.25 (0.18–0.34)	75	51
	Female	421 (360–482)	0.24 (0.18–0.30)	600 (477–878)	0.14 (0.09–0.20)	–	–

state of fish on the basis of visual inspection of gonads: fish with visible male or female gonads were classified as mature fish, and those with eggs present in the gonads were females (otherwise males). Fish with no visible gonads were classified as immature and of unknown sex. In addition, we collected the pair of sagittal otoliths to estimate ages of fish.

To ensure sufficient variation in lengths and ages for the subsequent growth analysis, for each area we compiled data on each group (i.e., immature fish, females, and males) by randomly selecting 5–10 fish per 20-mm size interval. Given the different ranges of pre-anal lengths of samples from Kengfang (range: 48–752 mm) and Tsukuan (75–379 mm), we selected 305 and 169 fish at the 2 areas, respectively. Further, because of a limited number of relatively small fish in the catch samples, we incorporated additional samples of small fish to conduct subsequent data analysis (no.=333 for Kengfang and no.=277 for Tsukuan).

Otolith processing and aging

There are generally no significant differences in otolith morphometrics between the left and right otoliths for a large number of fish species (Hunt, 1992; Megalofonou, 2006). Consequently, we randomly selected one of each pair of sagittal otoliths per fish, cleaned the surface of the otolith with an ultrasonic cleaning machine (Delta Sonicator DC150[4], Delta Ultrasonic Co., Ltd., Taipei, Taiwan), and air-dried and mounted it in epoxy resin blocks. We then ground the otolith resin blocks to reveal the otolith cores, using silicon carbon paper (grades 2000 or 2500).

We used the same aging techniques as those described in Shih et al. (2011): the otolith annuli were identified on the basis of the opaque bands. The first otolith annulus tended to be located at or beyond the

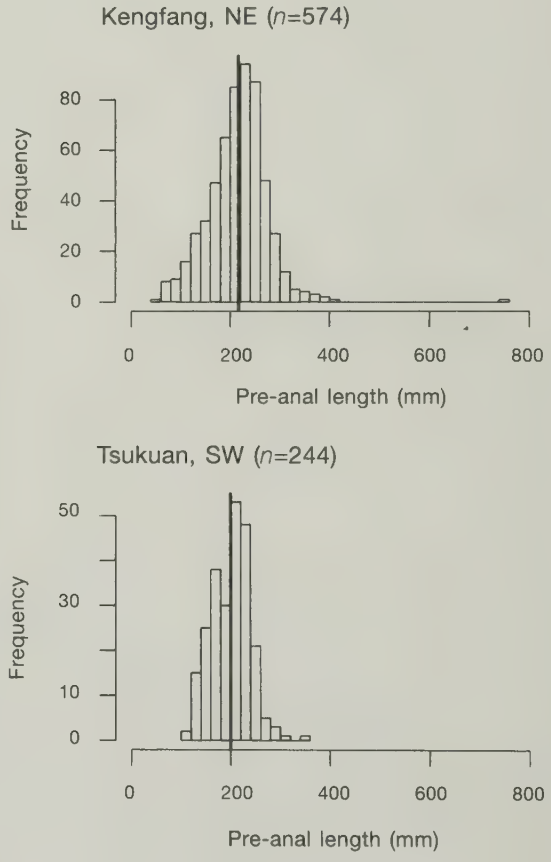

Figure 2

Length distributions of cutlassfish *Trichiurus japonicus* (males, females, and immature fish combined), sampled from the ports of (**A**) Kengfang and (**B**) Tsukuan, respectively, on the northeast (NE) and southwest (SW) coasts of Taiwan in 2013–2015. Vertical lines indicate mean lengths.

[4] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

half distance from the core to the edge (Suppl. Fig.) (online only). Two readers counted otolith annuli under a microscope at 200–400× magnification, examining each otolith independently. The otolith age estimates were inspected to determine whether the differences in age estimates between readers were >2 years. We excluded 47 otoliths because of otolith breaks or discrepancies >2 years between the 2 readings. After these otoliths were excluded, the rate of agreement in age estimates between the 2 readers was 85.5% (i.e., the 2 readings were the same for 501 of 586 otoliths). For subsequent analyses, we used the average values of the 2 age readings. However, because *T. japonicus* spawn year-round in the waters off Taiwan, the true age can vary among fish for an age estimate.

Data analysis

Growth We compared growth of *T. japonicus* between the areas on the basis of length-at-age data and by fitting a growth model. For the length-at-age comparison, we accounted for the effects of sex and stages of maturation on lengths. Therefore, we compared lengths at a given age for immature fish, males, and females between the areas by using a 2-sample *t*-test.

Given the prolonged, year-round spawning season of *T. japonicus* (Shih et al., 2011), months of birth for these fish could vary between the areas, resulting in bias for our comparison of growth. To account for such bias, we estimated daily ages, using otoliths for age-0 fish and compared their average daily growth rates between the 2 areas (number of fish sampled [*n*]=24 for Kengfang and *n*=20 for Tsukuan). One experienced reader assessed these otoliths 3 times independently, and the data were averaged after discrepant estimates between readings were excluded (e.g., difference ≥10 d). Because daily growth increments for fish of ages ≥1 year were too dense to be counted correctly, we could not estimate daily growth rates for older fish. We calculated individual average daily growth rates as the ratio of pre-anal lengths over average daily ages. For comparison, we derived another estimate of daily growth rates by fitting a linear regression of pre-anal lengths (y axis) in relation to daily ages (x axis) with a constant intercept of 5.5 mm for each area (i.e., corresponding to the length at hatching of *T. japonicus*; Kiang[5]). The regression slopes indicate the average daily growth rates. We evaluated differences in daily growth rates between the 2 areas by comparing the explained variance of pre-anal lengths of these 2 models: the model with both area and daily ages as predictors compared with the model with daily ages as the sole predictor.

To describe ontogenetic growth, we used the von Bertalanffy growth model (von Bertalanffy, 1938). Because of apparent size dimorphism of the sexes, we fitted this model separately for males and females in each area; immature fish were incorporated into samples of either sex for fitting sex-specific growth models. The von Bertalanffy growth model in terms of length is typically expressed as

$$L_t = L_\infty(1 - e^{-K(t-t_0)}),$$

where t = age, L_t is length at age t; and
L_∞ = asymptotic length;
K = the Brody growth coefficient; and
t_0 = the intercept at the horizontal axis (i.e., the hypothetical age at length 0).

Because of the lack of a biological meaning for t_0, it is common to replace it with L_0, the theoretical length at age 0. This leads to an alternative model form: $L_t=L_\infty-(L_\infty-L_0)e^{-Kt}$. This formulation is commonly applied to describe growth trajectories of elasmobranchs, given that their relatively large sizes at hatching can provide an adequate estimate of L_0 (Pardo et al., 2013). However, size at hatching is too small to be estimated accurately for many teleosts, including cutlassfish. Therefore, we substituted L_0 with L_{min}, the minimum length at catch. Accordingly, we offset all ages by t_{min}, the age corresponding with L_{min}, in the model:

$$L_t = L_\infty - (L_\infty - L_{min})e^{-K(t-t_{min})}. \quad (1)$$

The length-at-age data derived from length-stratified sampling may deviate from the true length-at-age distribution of a population. To avoid such bias and because measuring length is relatively precise and estimating age may not be, we estimated the von Bertalanffy growth parameters by using the inverse von Bertalanffy growth model, i.e., estimating age as a function of length (Vainikka et al., 2009; Mollet et al., 2013). The inverse function of Equation 1 is

$$t = t_{min} - \frac{1}{K}\ln\left(\frac{L_\infty - L_t}{L_\infty - L_{min}}\right). \quad (2)$$

The minimum lengths at catch (i.e., pre-anal lengths) of *T. japonicus* were 48 and 75 mm at Kengfang and Tsukuan (Table 1). By counting daily increments of these otoliths with 3 replicates, we estimated the mean of t_{min} to be 34 d (standard deviation [SD] 2.6) or 0.09 year and 51 d (SD 1.0) or 0.14 year at Kengfang and Tsukuan, respectively. Because a fish of length equal to L_{min} is immature and there is no reason to expect differential growth between sexes well before maturity, we assumed the same L_{min} and t_{min} for males and females. Inserting L_{min} and t_{min} into Equation 2, we used the nonlinear least squares method to estimate L_∞ and K for each sex and area. For comparison and compatibility with earlier studies, we also fitted Equation 1 to the length-at-age data.

We derived 95% confidence intervals (CIs) for the L_∞ and K estimates, using a bootstrap method (Manly, 1997). Specifically, we randomly sampled the length-at-age data with replacement to generate 1000 bootstrapped data sets, each with an equal sample size of the original data set, and then fitted Equations 1 and 2 to the bootstrapped samples. The lower and upper

[5] Kiang, Y.-K. 2017. Unpubl. data. National Taiwan Univ., No. 1, Sec. 4, Roosevelt Rd., Taipei, Taiwan 10617.

bounds of the 95% CIs of L_∞ and K were respectively the 25th and 975th quantiles of the 1000-bootstrap-derived values of L_∞ and K.

Age and length at 50% maturity Given that the maturity state is a binary variable and that probability of maturity tends to increase with length and age, we used logistic regression to estimate the age and length at which the probability of being mature is 50% (A_{50} and L_{50}). The equation that we used was

$$\text{logit}(p) = \ln\left(\frac{p}{1-p}\right) = \beta_0 + \beta_1 x, \quad (3)$$

where x = length or age; and
β_0 and β_1 are model coefficients.
A_{50} or L_{50} are the solutions of Equation 3 for p=0.5, that is, $-\beta_0/\beta_1$.

We derived the 95% CIs of A_{50} or L_{50} by using a bootstrap method (Manly, 1997). We generated 1000 bootstrapped data sets of equal sample size to those of the original data set and then fitted a logistic regression to the bootstrapped samples to derive estimates of A_{50} or L_{50}. The lower and upper bounds of the 95% CI of A_{50} or L_{50} were respectively the 25th and 975th quantiles of the 1000-bootstrap-derived values of A_{50} or L_{50}.

Probabilistic maturation reaction norms The PMRN approach involves estimating age- and length-specific probability of maturation with the use of a logistic regression (Heino et al., 2002). Because newly mature *T. japonicus* cannot be distinguished easily from those previously mature, we followed the demographic approach developed by Barot et al. (2004a, 2004b). This method is based on calculating change in length-specific maturity over a time interval, here 1 year, aligned by the average length increment over the time interval (ΔL). Specifically, we used data for a given age, sex, and area to fit a logistic regression with maturity status as a response and length as a predictor, separately for each age group:

$$\text{logit}(O_t) = \ln\left(\frac{O_t}{1-O_t}\right) = \beta_0 + \beta_1 L_t. \quad (4)$$

Equation 4 is equivalent to fitting Equation 3 to age-specific data.

O_t = the maturity ogive for age t;
L_t = length of fish at age t; and
β_0 and β_1 = the regression intercept and slope.

We fitted such a logit function of O_t for the ages in which both immature and mature individuals were present (i.e., t=1 and t=2 of both sexes and areas). Because of the relatively low number of age-specific samples (e.g., no.=19–58 per age-sex-location group), the logistic regression did not provide a good fit for some groups (i.e., age 1 of both sexes at Tsukuan, P=0.05–0.08). Nonetheless, we continued further analysis because these fits were reasonable on the basis of visual inspection (i.e., we accepted the model fits when the fitting lines represented increasing probability of maturity with fish length). Then, we estimated the age-specific probability of maturing (m):

$$m(L_t) = \frac{O_t(L_t) - O_{t-1}(L_t - \Delta L)}{1 - O_{t-1}(L_t - \Delta L)}. \quad (5)$$

Here the probability of maturing (m) is estimated as the fraction of immature fish at age t–1 that grew in length ΔL and reached maturity at age t. An underlying assumption of Equation 5 is that immature and mature fish of the same ages have the same growth and survival rates (Barot et al., 2004a, 2004b). Our data indicate that the lengths at ages 0, 1, and 2, respectively, did not vary between immature and mature fish of either sex in Kengfang but that the lengths varied between immature and mature male fish at ages 0, 1, and 2 in Tsukuan (Suppl. Table 3 (online only); this finding also is based on t-test results: P=0.01, 0.02, and 0.003 for ages 0 [n=20], 1 [n=49], and 2 [n=32], respectively). The observed differences in length at age between immature and mature fish indicate that our data violate this assumption. However, reports of previous studies have suggested that the PMRN approach was relatively robust even when this assumption is modestly violated (Barot et al., 2004a, 2004b).

The trajectory of probability of maturing generally indicates a sigmoid curve with increasing lengths. Therefore, we fitted a logistic regression with m as response and length as a predictor and estimated the length at m=0.5 (i.e., $Lp_{50,t}$):

$$\text{logit}(m(L_t)) = \beta_0 + \beta_1 \times L_t, \quad (6)$$

with $Lp_{50,t}$ obtained as the solution of Equation 6 for $m(L_t)$=0.5.

We estimated the 95% CIs of $Lp_{50,t}$ using the bootstrap method. We generated 1000 bootstrapped data sets of age t and age t–1 (each with equal sample size of the original data set) and used these data sets to derive 1000 estimates of $Lp_{50,t}$. The lower and upper bounds of the 95% CI of $Lp_{50,t}$ were the 25th and 975th quantiles of the 1000-bootstrap-simulated values of $Lp_{50,t}$.

Randomization tests Because parametric tests for comparing the von Bertalanffy growth coefficients (i.e., L_∞ and K) and maturation indices (i.e., A_{50}, L_{50}, and PMRNs) between the 2 sampling areas are cumbersome or unavailable, we used randomization tests (Manly, 1997; see also Barot et al., 2004b). Specifically, we permuted the data column of "area" and evaluated the between-area differences in the sex-specific estimates for each of these growth and maturation indices with 999 replicates. The sorted sequence of the 999 between-area differences of estimates approximated the range of all possible values of between-area differences for estimates under the null hypothesis (i.e., with no differences between the areas). We then evaluated the probability of the observed between-area difference for a sex-specific estimate (i.e., P-values) as $1-P(X \leq D)$, where D is the observed between-area difference. We

evaluated differences in growth and maturation between sexes using similar randomization tests.

Results

Length distribution and length at age

T. japonicus sampled in Kengfang (NE) were on average larger (mean pre-anal length: 216.0 mm [SD 60.3]) than fish from Tsukuan (SW; mean pre-anal length: 200.3 mm [SD 38.8]). Length distribution for Kengfang also was broader than that found for Tsukuan (coefficient of variation (CV): 28% versus 19%; Fig. 2).

We observed an ontogenetic shift in growth variation between the 2 areas. For immature fish at ages of 0 and 1 year, mean lengths were lower in Kengfang than in Tsukuan (Fig. 3A). Subsequently, for mature fish of both sexes at ages ≤2 years, differences in lengths between the areas were not significant (Fig. 3, B and C). However, the patterns of lengths at ages between the areas were partly reversed for fish at ages ≥3 years with greater lengths at age in Kengfang than in Tsukuan (Fig. 3, B and C).

Early juvenile growth

We estimated average daily ages for 17 and 19 age-0 fish in Kengfang (NE) and Tsukuan (SW), respectively (Suppl. Table 4) (online only). Average daily ages and pre-anal lengths of fish were higher in Tsukuan than in Kengfang (Suppl. Table 4; for daily ages, $|t|=3.56$, df=21, $P=0.002$; for pre-anal lengths, $|t|=2.63$, df=29.9, $P=0.01$). However, growth of very young *T. japonicus* was similar between the areas on the basis of both estimates of daily growth rates (see Suppl. Table 4 for the ratios of pre-anal-length to daily age, $|t|=0.41$, df=17.0, $P=0.68$; for the regression-based daily growth rate, $F=1.43$, $P=0.26$).

Growth model

The magnitudes of area- and-sex-specific estimates of L_∞ and K varied greatly between the 2 different model fits (e.g., Equations 1–2; Table 1). However, for output from both models, consistent growth patterns between the areas and sexes were observed (Table 1; Fig. 4). Generally speaking, L_∞ was higher and K lower in Kengfang (NE) than in Tsukuan (SW). Females had higher L_∞ and lower K than those of males (Table 1; Fig. 4). On the basis of randomization tests, the between-area differences in both L_∞ and K were significant for both models: for L_∞ of Equation 1, $P<0.001$ for males and $P=0.002$ for females; for L_∞ of Equation 2, $P<0.001$ for males and $P=0.008$ for females; for K of Equation 1, $P<0.001$ for males and $P=0.003$ for females; and for K of Equation 2, $P<0.001$ for males and $P=0.003$ for females (Table 1; results of randomization tests of between-sex differences in L_∞ and K are shown in Suppl. Table 5) (online only). These differences are in

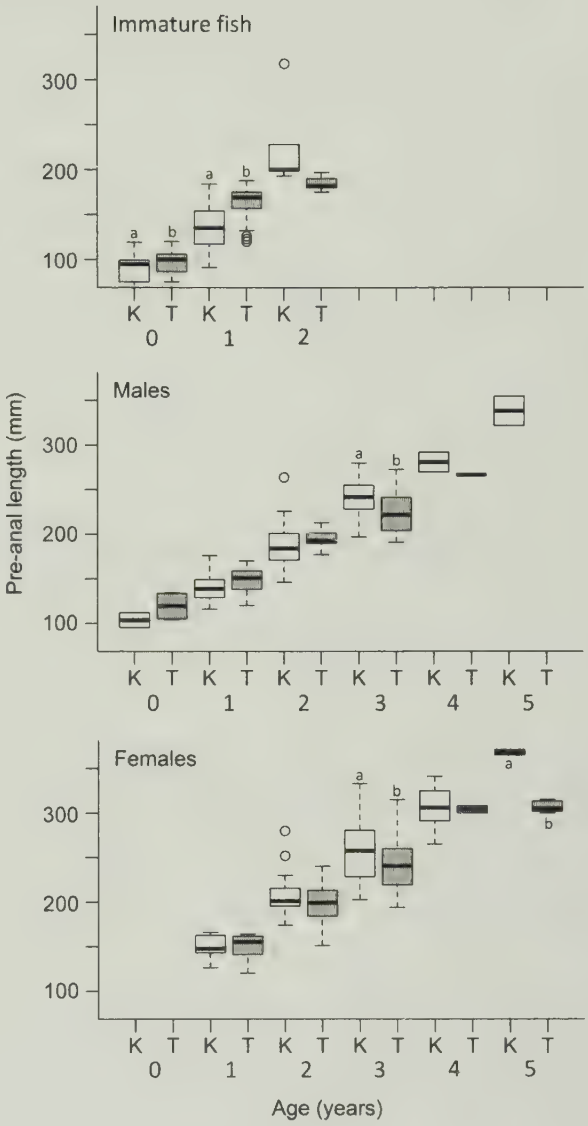

Figure 3

Length-at-age comparisons between 2 fishing areas off Taiwan near the ports of Kengfang (K, open boxes) and Tsukuan (T, gray boxes), based on sex- and maturation-state-specific data for (**A**) immature (**B**) male, and (**C**) female cutlassfish, *Trichiurus japonicus*, sampled in 2013–2015. The secondary x-axis shows the age group of fish. The letters *a* and *b* denote significant differences between the areas based on *t*-test results for immature fish at age 0 ($|t|=2.01$, df=35.9, $P=0.05$), immature fish at age 1 ($|t|=4.67$, df=61.4, $P<0.001$), males at age 3 ($|t|=3.08$, df=61.0, $P=0.003$), females at age 3 ($|t|=2.29$, df=91.9, P 0.02), and females at age 5 ($|t|=15.73$, df=2.7, $P=0.001$).

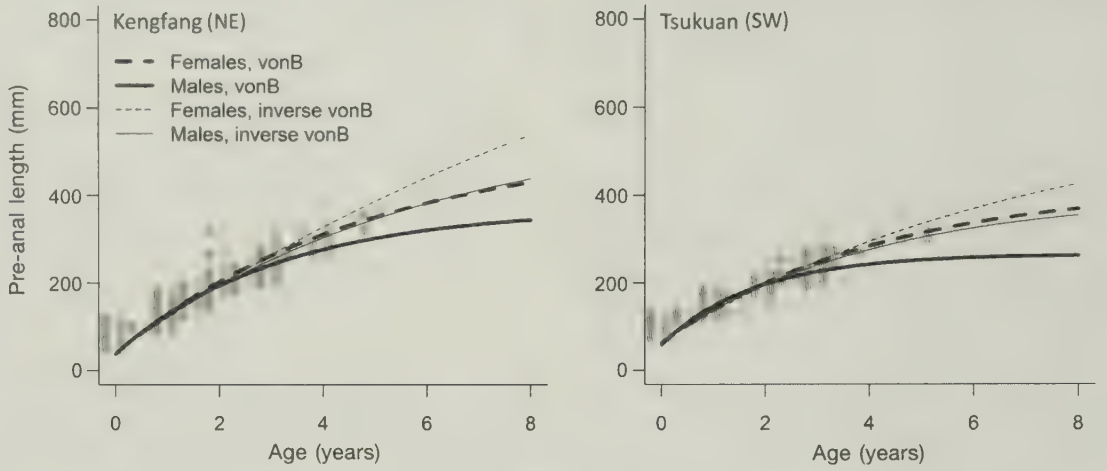

Figure 4

Sex-specific growth trajectories for populations of a cutlassfish, *Trichiurus japonicus*, near the ports of Kengfang and Tsukuan off the northeast and southwest coasts of Taiwan, derived from both the von Bertalanffy growth model (vonB, thick black lines) and the inverse model (inverse vonB, thin gray lines). For Kengfang data, one female sample with a large pre-anal length (752 mm) was excluded prior to fitting regression to enhance quality of fitting given the very high leverage and some uncertainty in the age estimate for this fish.

agreement with the general patterns of larger length at age for older fish in Kengfang than Tsukuan (Fig. 3, B and C); however, for early ages, the larger K for *T. japonicus* in Tsukuan compensates for their lower L_∞, in agreement with length at age of immature fish being larger in Tsukuan than in Kengfang (Fig. 3A).

Age and length at 50% maturity

The estimates of A_{50} and L_{50} indicate consistent patterns between the areas and sexes: fish taken in Kengfang (NE) were older and larger at 50% maturity than those collected in Tsukuan (SW), and females reached 50% maturity at older ages and larger lengths than males (Fig. 5). Nonetheless, randomization tests revealed between-area differences in A_{50} and L_{50} were significant for males (P=0.005 and P=0.014 for A_{50} and L_{50}, respectively) but not for females (P=0.116 and P=0.066 for A_{50} and L_{50}, respectively; results of randomization tests of between-sex differences in A_{50} and L_{50} are shown in Suppl. Table 5) (online only). When data for the 2 areas were combined, ranges of A_{50} and L_{50} were 1.2–1.7 years and 153–184 mm, respectively.

Probabilistic maturation reaction norms

The PMRNs could be estimated for *T. japonicus* at ages of 1–2 years for both sexes and areas (Fig. 6), encompassing the age range during which 50% maturity was reached (Fig. 5). The 95% CIs of the sex- and area-specific midpoints of PMRNs overlapped (Fig. 6). Randomization tests showed no significant differences in these midpoints of PMRNs between sexes or areas

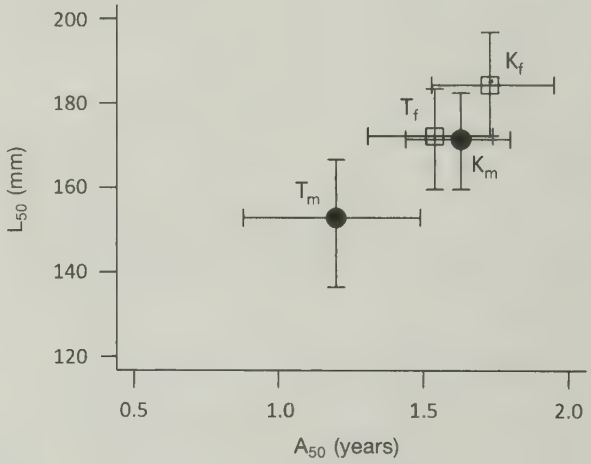

Figure 5

Estimates of length and age at 50% maturity (L_{50} and A_{50}) for populations of a cutlassfish, *Trichiurus japonicus*, sampled at the ports of Kengfang (K) and Tsukuan (T) in Taiwan in 2013–2015. Open squares indicate estimates for females (f), and black circles indicate values for males (m). Error bars indicate bootstrap-derived 95% confidence intervals.

(between-areas: P=0.24 and P=0.25 for males at ages 1 and 2, respectively; P=0.09 and P=0.44 for females at ages 1 and 2, respectively; for between-sexes randomization tests, see Suppl. Table 5) (online only).

Comparison of the midpoints of PMRNs and the

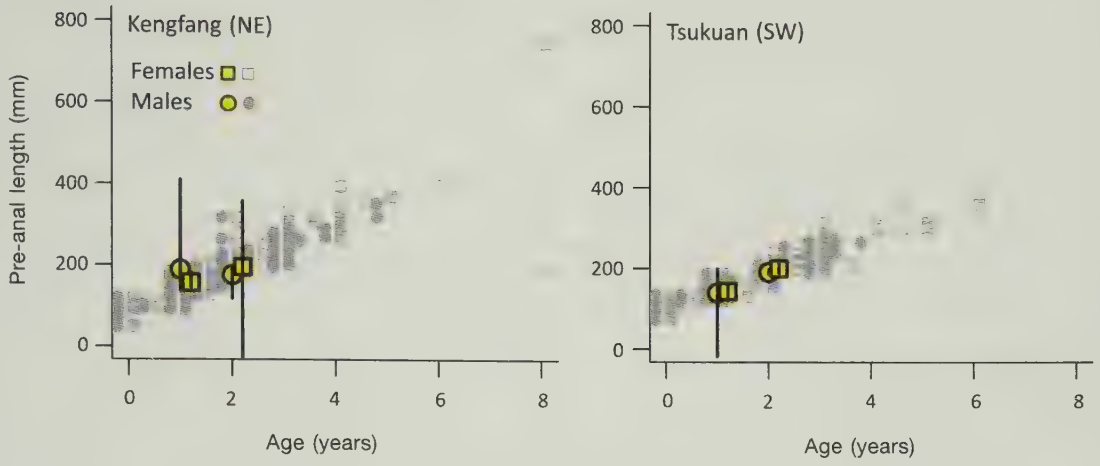

Figure 6

Estimates of probabilistic maturation reaction norms (yellow symbols) with length-at-age data (gray symbols) for populations of a cutlassfish, *Trichiurus japonicus* (females and males), sampled at the ports of Kengfang and Tsukuan on the northeast and southwest coasts of Taiwan in 2013–2015. Vertical black lines indicate bootstrap-derived 95% confidence intervals.

corresponding sex- and area-specific growth data at ages 1 and 2 revealed some phenotypic differences in maturation between the areas. As Figure 5 shows, the earliest maturation occurs in Tsukuan males (SW). In agreement with this observation, the males in Tsukuan have a relatively low PMRN midpoint, together with relatively large lengths for immature fish at age 1 (see Fig. 3A), resulting in a relatively high likelihood of maturation at that age. In contrast, for males in Kengfang (NE), the PMRN midpoint for age 1 was greater than the lengths of most age-1 individuals, resulting in a greater tendency to have delayed maturation to age 2 (Fig. 5, Fig. 6A). For female fish, between-area differences in the midpoints of PMRNs were so small (Fig. 6) that the difference in length of immature fish did not result in clear differences in maturation.

Discussion

Our study provides evidence of variation in growth and maturation patterns and potential underlying drivers of those patterns for a subtropical cutlassfish at a small spatial scale. We found that growth rates of the early stage of juvenile *T. japonicus* (first few months) were similar between areas, whereas immature fish at ages of 0–1 years grew faster in the warmer Tsukuan (SW), corresponding to the spatial gradient of temperatures. However, results for growth of adults indicate an inverse pattern and that both adult males and females tended to be larger in the colder Kengfang (NE). Further, we found that *T. japonicus* generally matured at ages 1–2 in both areas, but males in Kengfang had a tendency for delayed maturation. Because the midpoints of PMRNs did not differ significantly between the areas, growth-related phenotypic plasticity is sufficient to explain the observed variation in maturation schedules of males. This result contrasts with those from some earlier studies in which neighboring stocks or stock components were compared (marine fish: Olsen et al., 2005; Vainikka et al., 2009; Wright et al., 2011; Mollet et al., 2013; freshwater fish: Wang et al., 2008; Morita et al., 2009). Overall, these observed patterns of differences in growth and maturation between the areas are consistent with the temperature-size rule (Angilletta et al., 2004; Arendt, 2011), where cooler temperatures led to slower prematuration growth, delayed maturation, and larger asymptotic lengths for fish. However, with the comparison of only 2 fishing grounds and limited environmental data, we cannot exclude other sources that could produce plastic variation.

Temperature-size rule involves thermal effects on growth and maturation

A negative effect of temperature on adult body size, the temperature-size rule has been reported for various organisms (Atkinson, 1994; Angilletta et al., 2004). Such an effect of temperature on variation in body size may involve multiple plastic or adaptive pathways (Angilletta et al., 2004; Ohlberger, 2013). For example, temperature may induce plastic changes in physiological rates, such as growth, metabolism, and mortality and lead to the observed variation in body size (e.g., Munch and Salinas, 2009). Simultaneously, temperature effects on the metabolic rates may induce adaptive changes. As metabolic costs increase with temperature, a thermal constraint on maximum body size may oc-

cur at warm temperatures. Consequently, selection should favor differential optimal adult body sizes with respect to the temperature differences (Berrigan and Charnov, 1994; Atkinson, 1996). Moreover, several authors suggest that the temperature-size patterns may involve changes in the reaction norms of growth and maturation (Angilletta et al., 2004; Ohlberger, 2013). In relation to these studies, our results provide a clear evidence of the covariation of growth and maturation underlying the temperature effects on adult body sizes. Additionally, we show that some variation in these life-history traits (e.g., maturation) is likely to be chiefly plastic.

Other sources of life-history variation

Potentially, other factors may also contribute to the observed life-history variation in *T. japonicus*. For example, positively size-selective fishing may induce selection for growth, favoring the genotypes associated with slower growth rates (Ricker, 1981; Conover and Munch, 2002; Reznick and Ghalambor, 2005; Wang and Höök, 2009; Enberg et al., 2012). Also, fishing-induced size truncation of adult demography (Hsieh et al., 2010) could potentially confound the patterns of differences in growth between the areas. The different length distributions (Fig. 2) indicate higher mortality for fish along the SW than along the NE coast—a finding that is consistent with the higher fishing power of the vessels operating from Tsukuan in comparison with those from Kenfang. However, because estimates of fishing mortality for cutlassfish in Taiwan were unavailable, it remains unclear whether different fishing intensity accounts for the life-history variation in cutlassfish between the areas. To enhance understanding of growth patterns for *T. japonicus*, we suggest identifying other relevant driving factors that affect growth of cutlassfish (e.g., fishing and other biological interactions).

We found that between-area variation in maturation schedules was more pronounced for males than females. In general, increasing body size tends to increase fitness more for female fish than for male fish (Bell, 1980; Gross and Sargent, 1985; Fleming and Gross, 1994). Consequently, selection may favor delayed maturation in females, compensating for the different growth rates between the areas.

Our results indicate potential adaptive variation in adult growth rates and plastic variation in maturation of *T. japonicus* between 2 areas off Taiwan. The spatial patterns of adult growth rates and maturation follow the temperature gradient, indicating that temperature variability exerts an effect on the observed life-history patterns. Also, the different adult growth rates between sexes are consistent with selection that favors sexual dimorphism with body size (Parker, 1992).

Implications for fisheries management

Adaptive and plastic variation in life-history traits are evidence of the complex effects of environmental and anthropogenic drivers on living organisms. Consequently, it is critical to understand the processes that lead to variation in life-history characteristics in order to enhance the effectiveness of natural resource management. Subtropical and tropical fishes are under much pressure from both environmental changes and fisheries exploitation (Cheung et al., 2010; Blanchard et al., 2012). Our results provide essential information on how a subtropical fish responds to these effects, information (e.g., accounting for the area-specific life-history patterns and the regulation of fishing intensity) that can be incorporated in potential management plans.

Our results indicate that there is a significant difference in growth trajectories for *T. japonicus* from the 2 primary fishing grounds in Taiwan. Such distinct growth patterns indicate the possible presence of discrete populations, and this result is in agreement with broad-scale patterns in mitochondrial DNA markers (Tzeng et al., 2016). On the other hand, we did not find significant differences in the PMRNs, which might be expected to mirror observed genetic differences. A better understanding of the spatial scales of population differentiation and the roles of genetic and plastic variation in life-history traits of this important commercial species is clearly needed.

There is increasing concern about the potential warming of ocean waters and the effects of this warming on body size of various organisms, including commercially caught fish (Sheridan and Bickford, 2011; Baudron et al., 2014). Our findings contribute to an understanding of the mechanisms underlying such warming effects through the documentation of differences in growth rates of the *T. japonicus* that experience different temperature regimes in the 2 sampling areas. Moreover, we suggest that the information on temperature–size (life-history) relationships may be useful for forecasting changes in sizes of other subtropical fish species.

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Age and growth rates at the early life stages of common pandora (*Pagellus erythrinus*) based on analysis of otolith microstructure

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Abstract—We investigated young-of-the-year (YOY) growth, age, and hatching distributions of common pandora (*Pagellus erythrinus*) by analyzing otolith microstructure. This study was carried out in shallow waters (0–20 m) off the island of Gökçeada, Turkey, from June 2013 through June 2014. A total of 231 YOY common pandora were measured and aged. These fish ranged from 12 to 110 mm in total length and from 38 through 242 d in age. The indices for determining variability in daily age estimates (average percentage error and coefficient of variation) were 4.9% and 3.4%, respectively. Average daily growth rate was calculated from a linear regression of the age–length data set as 0.52 mm/d. A linear relationship was found between otolith morphometric measurements (otolith length, width, and radius) and total length for YOY common pandora. The hatching times of common pandora were back-calculated to occur from February through October, and 2 main hatching cohorts were evident in spring (March) and summer (August).

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The common pandora (*Pagellus erythrinus*) is distributed throughout the Mediterranean Sea and the northeastern Atlantic Ocean from Norway to Cape Verde (Bauchot and Hureau, 1986; Whitehead et al., 1984–1986). This fish is a protogynous hermaphrodite, and individuals are first female and become male in the third or fourth year of life. The length of time of sex reversal for common pandora is different among the different regions of the Mediterranean Sea (Zei and Županović, 1961; Klaoudatos and Klaoudatos, 2004; Zarrad et al., 2010; Saoudi et al., 2017). This species inhabits shallow waters down to 120 m, mostly among rock, gravel, and sandy–muddy sediments (Jukić and Arneri, 1984; Papaconstantinou et al., 1988). The spawning period of this species has been reported to occur from spring to early autumn depending on region and hydrological conditions (Pajuelo and Lorenzo, 1998; Coelho et al., 2010; Metin et al., 2011).

The common pandora is a high-value species among the porgies (Sparidae) (Coelho et al., 2010). This species is an important demersal resource throughout the Mediterranean Sea and Black Sea. The common pandora is caught in trawls, trammel nets, gill nets, bottom long lines, and hand lines (Metin et al., 2011). Fishing pressure and increased adult mortality have resulted in earlier maturity at a smaller size (Beverton and Holt, 1956). Size at first maturity of the common pandora has been reported to be 11–16 cm in total length (TL) in the Aegean Sea (Metin et al., 2011), 14–16 cm TL in the central Mediterranean Sea (Zarrad et al., 2010; Ali Ben Smida et al., 2014), 17–18 cm TL off Portugal (Coelho et al., 2010), and 17–23 cm TL off the Canary Islands (Pajuelo and Lorenzo, 1998).

Information on population parameters, such as daily age, growth, and hatching times of heavily exploited fish species provide important information for stock assessments and fishery management (Aliaume et al., 2000). The common pandora is listed in the IUCN Red List of Threatened Species as a species of least concern (Russell, 2014). Despite the wide distribution and ecological and economic importance of this species, most studies on the age and growth rates of this species have focused on adult individuals, and there is no study on age and growth of early life stages. However, information on early life stages is essential for understanding population traits, such as recruitment and productivity.

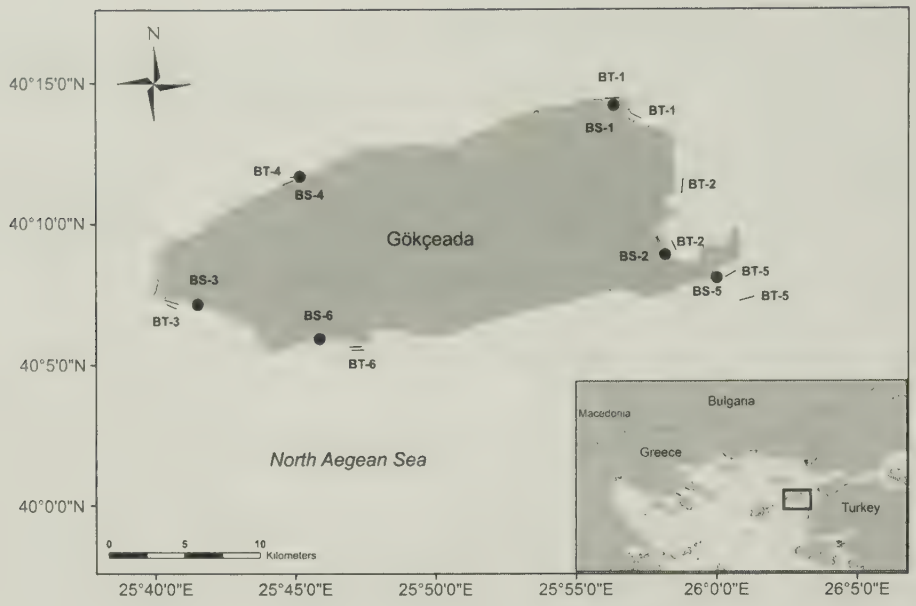

Figure 1

Six sampling stations where young-of-the-year common pandora (*Pagellus erythrinus*) were collected with beach seine (BS) or beam trawl (BT) from the shallow waters (<20 m) off the island of Gökçeada, Turkey, from June 2013 through June 2014.

In this study, we investigated young-of-the-year (YOY) age, growth rates, and back-calculated hatching dates of common pandora collected from the island of Gökçeada, Turkey, by analyzing their otolith microstructure. We also examined the relationships between otolith morphometric measurements (length, width, and radius) and fish total length.

Materials and methods

During the daytime, YOY common pandora were collected with a beach seine and beam trawl from 6 sites in shallow waters (<20 m) off Gökçeada, Turkey (Fig. 1). Samples were taken from June 2013 through June 2014. Beam trawling speed was 2–3 kt. The beach seine hauls were made parallel to the shore.

Total length of common pandora was measured to the nearest 1 mm, and total weight was measured with a digital balance with precision to 0.01 g. A total of 261 pairs of sagittal otoliths were removed, cleaned, and placed in clean, labeled vials. One otolith of the sagittal pair was randomly selected and subsequently embedded in epoxy resin, mounted on a glass slide, and ground to expose the core (Miller and Storck, 1982; Secor et al.[1]; Jones, 1992; Hayes, 1995).

Otolith daily growth rings were counted from the core to the outer edge under a light microscope at magnifications of 40× and 100× (Fig. 2). The number of daily increments between right and left otoliths were compared with a paired *t*-test. Two readers independently counted the daily rings without prior knowledge of fish length, and, when counts differed from each other by more than 10%, these otoliths were not included in the study.

Estimates of the precision of daily growth ring counts between readers were determined by using the average percentage error (APE) of Beamish and Fournier (1981) and coefficient of variation (CV) (Chang, 1982).

It was assumed that growth increments in the sagittal otoliths are formed daily. Daily ring formation has not been validated for common pandora; however, it has been validated for many fish species (Pannella, 1971; Campana and Neilson, 1985). The slope of the regression analysis of the TL and the number of otolith daily growth rings was used to estimate the overall YOY growth rates. Daily growth rates for the capture date of each cohort (except when the number of samples (n) was <5, see Table 3) also were estimated by fitting a linear model. The differences in slopes were compared by using an analysis of covariance (ANCOVA) to identify the significant differences in daily growth for each cohort.

Otolith morphometric measurements (otolith length [OL], width [OW], and radius [OR]) were measured to the nearest 0.001 mm by using QCapture Pro[2] imaging

[1] Secor, D. H., J. M. Dean, and E. H. Laban. 1991. Manual for otolith removal and preparation for microstructural examination. Belle W. Baruch Inst. Mar. Biol. Coast. Res., Tech. Publ. 1991-01, 55 p. [Available from Belle W. Baruch Inst. Mar. Coast. Sci., Univ. South Carolina, Columbia, SC 29208.]

[2] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

Table 1

Summary of the total lengths in millimeters of young-of-the-year common Pandora (*Pagellus erythrinus*) collected in the shallow waters (<20 m) off Gökçeada, Turkey, from June 2013 through June 2014. The number of specimens (*n*) and range, mean, and standard error of the mean (SE) for total length are provided.

Month of capture	*n*	Min	Max	Mean	SE
March	3	51	82	65.67	8.99
April	1	110	110	110.00	...
May	1	85	85	85.00	...
June	42	15	73	45.33	1.97
July	67	12	80	41.73	2.37
August	34	25	70	47.47	2.08
September	3	18	33	25.33	4.33
October	43	13	98	25.74	2.93
November	66	16	86	32.98	1.88
December	1	43	43	43.00	...

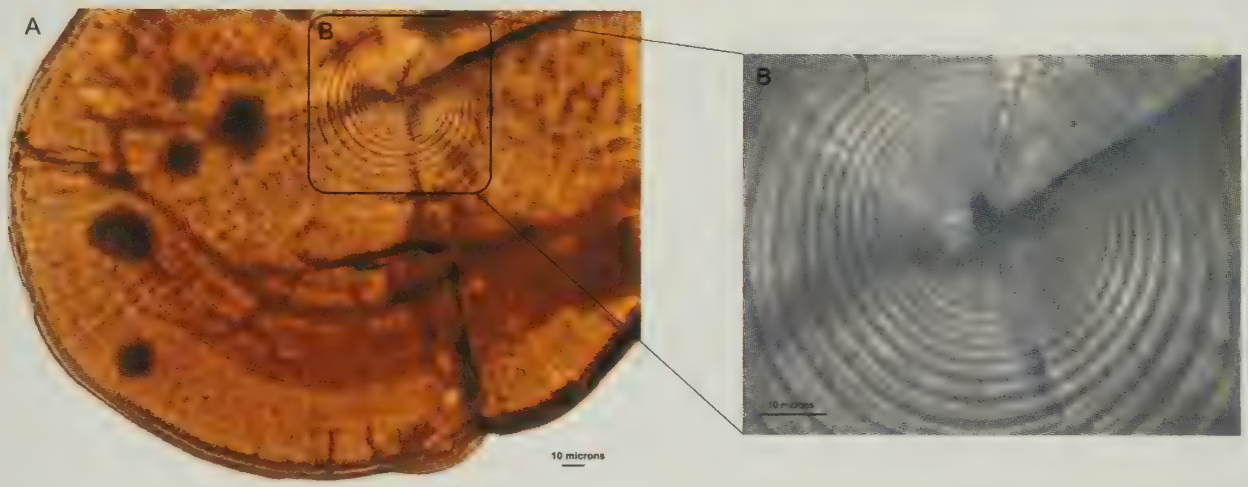

Figure 2

(**A**) Images of the daily growth rings seen in a polished sagittal otolith of a young-of-the-year common pandora (*Pagellus erythrinus*) collected in November 2013 off Gökçeada, Turkey. (**B**) Showing the otolith core. This fish was aged at 59 d and had a total length of 22 mm.

software (vers. 5.1; QImaging, Surrey, Canada). Otolith length is the longest axis between the anterior and posterior otolith edge, and OW is the distance from the dorsal to the ventral edge. Otolith radius is the longest axis between the core and posterior edge. A linear regression was used to describe the relationship between fish TL and otolith morphometric measurements for YOY common pandora.

Distributions of hatching dates of YOY common pandora were back-calculated from daily age estimates and date of capture. No mortality correction was applied to the hatching-date distributions (Campana and Jones, 1992).

Results

A total of 261 YOY common pandora were sampled from shallow waters off the island of Gökçeada. Young-of-the-year fish ranged in size from 12 to 110 mm TL (Table 1). Thirty pairs of sagittal otoliths were rejected because they were over ground or cracked, or there were discrepancies in daily ring counts among the age readers. Daily ages were determined successfully from 231 otoliths of YOY common pandora that ranged in size from 12 to 110 mm TL. We found that the average length of specimens increased with bottom depth (Fig. 3).

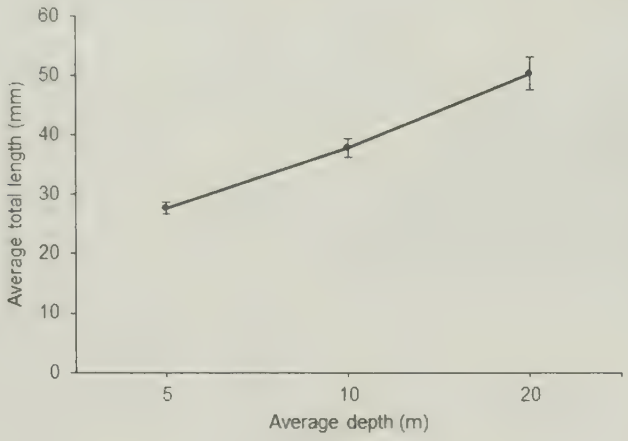

Figure 3

Relationships between average depth and mean total lengths of young-of-the-year common pandora (*Pagellus erythrinus*) collected off Gökçeada, Turkey, during June 2013–June 2014.

Table 2

Parameters of the linear relationship of the different otolith morphometric measurements, otolith length (OL), otolith width (OW), and otolith radius (OR), with fish length for young-of-the-year common pandora (*Pagellus erythrinus*) collected off Gökçeada, Turkey, during June 2013–June 2014. The number of specimens (n), y-intercept (a), slope of the regression line (b), and coefficient of determination (r^2) are provided.

Morphometric measurements	n	a	b	r^2	P
OL	228	2.407	21.271	0.975	<0.01
OW	228	2.702	30.315	0.961	<0.01
OR	198	4.249	41.875	0.942	<0.01

There was no significant difference between the numbers of daily growth increments counted for the left and right otoliths (paired t-test: n=30, P>0.05). Therefore, only one otolith was randomly selected for daily age estimation. The maximum observed age was 242 d (for a fish at 110 mm TL), and the minimum observed age was 38 d (for a fish at 12 mm TL). The age group 58–77 d (for fish at 18–41 mm TL) was dominant (25.5%). Specimens of age groups 198–217 and 218–237 were absent. The APE and CV were calculated as 4.9% and 3.4%, respectively.

Sagittal otolith length, width, and radius were observed in the ranges of 0.37–7.07 mm, 0.26–5.03 mm, and 0.18–3.59 mm, respectively. Relationships between TL and otolith morphometric measurements (OL, OW, and OR) were described by linear equations (Table 2).

The daily growth rate of YOY common pandora was estimated as 0.52 mm/d (Fig. 4). The maximum daily growth rate of 0.54 mm/d was found in the June cohort, and the minimum value of 0.46 mm/d was observed in the August cohort (Table 3). However, there were no statistically significant differences in either slope or adjusted mean among the equations (ANCOVA: F=1.216, df=4, P=0.305).

Spawning of YOY common pandora took place in 2 peaks represented by overlapping normal distributions (Fig. 5). The first spawning peak was observed in

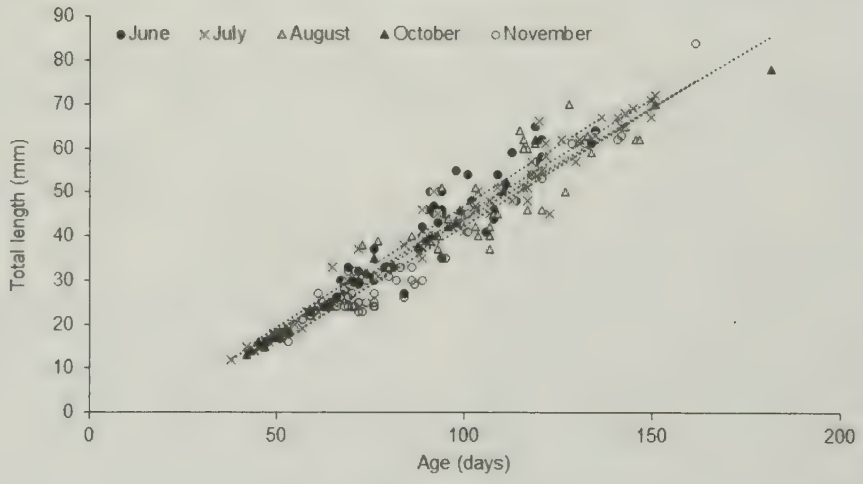

Figure 4

Age–length relationships estimated for young-of-the-year common pandora (*Pagellus erythrinus*) collected off Gökçeada, Turkey during June 2013–June 2014.

Table 3

Parameters of the linear models for the relationship between total length (TL) and number of daily increments (age) for young-of-the-year common pandora (*Pagellus erythrinus*) collected off Gökçeada, Turkey, during June 2013–June 2014. The number of specimens (n), size and age range with standard error of the mean (SE), y-intercept (a), slope of the regression line (b), and coefficient of determination (r^2) are provided. Capture months during which less than 5 specimens were collected are not included.

Month of capture	n	Size (mm TL)	SE	Number of daily increments (age)	SE	a	b	r^2	P
June	42	15–73	1.97	46–137	3.14	8.17	0.54	0.84	<0.01
July	67	42–63	2.37	38–151	4.25	8.06	0.52	0.96	<0.01
August	34	25–70	2.08	64–147	3.85	1.55	0.46	0.73	<0.01
October	43	13–98	2.93	42–182	5.48	7.30	0.50	0.97	<0.01
November	66	16–86	1.88	51–162	2.79	11.55	0.53	0.92	<0.01
All	231	12–110	21.12	38–242	31.59	8.41	0.52	0.93	<0.01

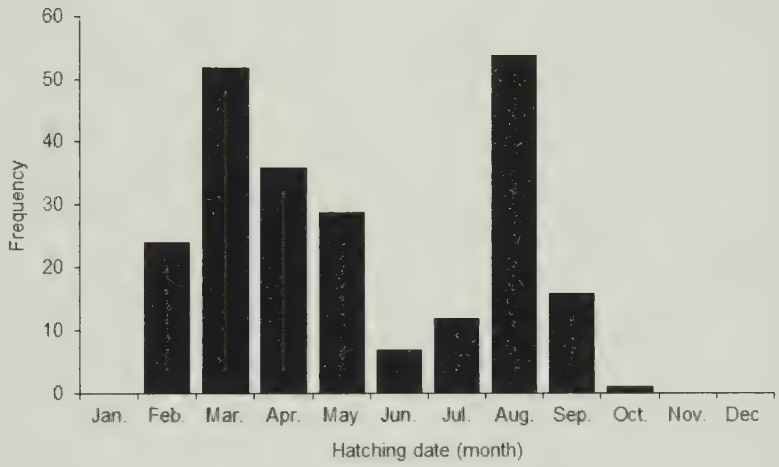

Figure 5

Hatching-date frequency distributions back-calculated by using age estimates and sampling dates of young-of-the-year common pandora (*Pagellus erythrinus*) collected off Gökçeada, Turkey, during June 2013–June 2014.

spring (March), and the second one was seen in summer (August). The hatching times of common pandora were back-calculated to occur between February and October.

Discussion

This study provides the first estimates of daily age and growth rates for the YOY of common pandora. Distinct light and dark bands, which can be used for age determination, were observed in the examined otoliths of YOY common pandora. Daily increment formation in otoliths is a general phenomenon that has been validated for many other species (Pannella, 1971; Campana and Neilson, 1985; Jones, 1992). Therefore, formation of increments on the otoliths of common pandora were assumed to occur daily. Campana (2001) suggested that acceptable levels for APE and CV were 5.5% and 7.6%, respectively. Therefore, our results (4.9% and 3.4%, respectively) are close to the acceptable values for both APE and CV.

Our findings are consistent with those of Somarakis and Machias (2002), who reported that the mean sizes of common pandora increased with bottom depth because smaller individuals were found in shallower and warmer waters. Few researchers have also addressed whether the decline in the number of older fish may

not only be due to mortality but also partially to movements of larger fish to deeper waters (Harmelin-Vivien et al., 1995; Ayyildiz et al., 2015).

No previous studies have used otolith microstructure analysis on age and growth rates of the early life stages of the common pandora. Therefore, we compared the data from our study of common pandora at early life stages with lengths at age 0 reported for adult common pandora in previous studies. The results of a recent study by Somarakis and Machias (2002) indicate that common pandora can reach a size of 120 mm TL at age 0. Similarly, a specimen of common pandora with a size of 100 mm TL was found at age 0 by Pajuelo and Lorenzo (1998). These results are supported by Hoşsucu and Çakır (2003), who found that average size at age 0 of common pandora was 77–78 mm TL and average size at 1 year of age was 117–119 mm TL. The results of our study match those observed in these earlier studies.

It is possible to estimate the length of fish by using morphometric measurements of otoliths (Harvey et al., 2000; Campana, 2004; Zan et al., 2015). Morphometric characteristics of the sagittal otoliths of YOY common pandora were linearly related to the logarithm of fish TL. Our results are consistent with those of other studies and indicate that the relationships between fish TL and otolith morphometric measurements are usually log linear (Ayyildiz et al., 2014; Dehghani et al., 2016; Al-Busaidi et al., 2017). However, according to Lleonart et al. (2000), the linear model is not appropriate because it cannot detect changes in the shape of otoliths.

The hatching times of common pandora were back-calculated to occur between February and October, and 2 main cohorts were estimated to occur in the spring (March) and summer (August). This result broadly agrees with the findings of Hoşsucu and Çakır (2003) and Zarrad et al. (2010) that indicate that the reproductive season of common pandora extended from April to October. Several studies also have revealed that the duration of the reproductive season of common pandora extends from April to September and peak spawning activity occurs between June and August (Pajuelo and Lorenzo, 1998; Valdés et al., 2004). A recent study by Coelho et al. (2010) reported a similar reproductive spawning season from March to July.

Acknowledgments

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The effect of reduced data on the ability to monitor rebuilding of overfished fish stocks

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Abstract—Several rockfish stocks off the U.S. west coast are below target biomass and are managed under rebuilding plans that severely limit the allowable harvest. Limited harvest, however, reduces the opportunity to collect fishery-dependent data, which are the primary source of information on changes in abundance for species poorly sampled by fishery-independent methods. A simulation study was conducted by using an operating model to evaluate the effect of reduced data on estimation of spawning biomass and biological parameters during rebuilding of a stock. Decreased availability of data during rebuilding resulted in increased among-simulation variation in estimates of spawning biomass. Additionally, decreased data resulted in reduced average catches and increased interannual variation in catches during rebuilding compared with averages of and variation in catches when data collection was maintained at higher levels. The presence of time-varying parameters in the operating model that were not accounted for within the estimation method resulted in increased among-simulation variability in spawning biomass than with the time-invariant case, and the largest increase in variability occurred during stock rebuilding when data were reduced or eliminated. Retaining data collections at historical levels allowed improved parameter estimation during rebuilding, resulting in reduced variability in estimated stock size, increased average catches during rebuilding, and in reduced frequency of stocks being prematurely estimated as rebuilt.

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In the United States, federally managed stocks that fall below a minimum stock size threshold (MSST) are declared overfished and are mandated to be rebuilt to target biomass levels in the shortest amount of time, accounting for present biological and environmental conditions (Sustainable...1996; National...2016). In the absence of an unexpected run of good recruitment, rebuilding overfished stocks requires a reduction in fishing mortality to a level that allows stock biomass to increase and therefore leads to substantial reductions in fishing effort in relation to historical levels. The severity of management restrictions during rebuilding can, for some stocks, lead to a situation where the ability to collect data becomes limited when the stock is under a rebuilding plan, a period when managers are likely most concerned about stock size and trends in biomass.

Overfished rockfish species off the U.S. west coast have experienced large reductions in harvest during rebuilding. One example, yelloweye rockfish (*Sebastes ruberrimus*), was declared overfished in 2002 (Methot and Piner[1]). Similar to other rockfish species off the U.S. west coast, catches of yelloweye rockfish were unsustainable during the 1980s and early 1990s. Catches of yelloweye rockfish decreased dramatically in relation to historical catches after the overfished declaration, and the allowable catch during the first year of rebuilding fell to approximately 10% of the catch from 4 years earlier (Stewart et al.[2]). Yelloweye rockfish is one notable example of an overfished west coast rockfish species that has experienced similar large reductions in harvest during rebuilding. Other examples include the cowcod (*Sebastes levis*; Dick and MacCall[3]), canary

[1] Methot, R., and K. Piner. 2002. Rebuilding analysis for yelloweye rockfish: update to incorporate results of coastwide assessment in 2002, 11 p. Pacific Fishery Management Council, Portland, OR. [Available from website.]

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Table 1

Life-history and observation parameters used in the operating model and their treatment within the estimation method to simulate a rockfish life-history type common to the west coast of the United States.

Parameter	Time-invariant	Time-varying	Treatment in estimation method
Natural mortality (M) per year	0.08	0.08	Fixed
Natural mortality standard error (σ_m)	0	0.10	
Natural mortality autocorrelation (ρ)	0	0.707	
Steepness (h)	0.65	0.65	Estimated
Maximum length (L_∞) (cm)	64	64	Estimated
Growth coefficient (K)	0.05	0.05	Estimated
Weight at length $w_l = \alpha L^\beta$ (kg)	α=0.50×10^{-5}, β=3	α=1.50×10^{-5}, β=3	Fixed
Length at 50% maturity (cm)	37	37	Fixed
Recruitment variation (σ_R)	0.50	0.50	Fixed
Fishery CPUE standard error (σ_f)	0.30	0.30	Fixed
Fishery CPUE catchability coefficient (Q_f)	0.01	0.01	Analytically estimated
Width at maximum selectivity (cm)	−3	−3	Estimated
Width at maximum selectivity standard error (σ_w)	0	0.20	
Size at maximum selectivity (cm)	45	45	Estimated
Size at maximum selectivity standard error (σ_s)	0	0.05	

rockfish (*Sebastes pinniger*; Thorson and Wetzel[4]), and Pacific ocean perch (*Sebastes alutus*; Hamel and Ono[5]).

The reduction of fishery catch, and of the resulting fishery data during rebuilding, presents a challenge for assessment and management of rebuilding stocks. Many species of rockfish off the U.S. west coast (e.g., cowcod, yelloweye rockfish) are not reliably sampled by the main fishery-independent survey, the NOAA Northwest Fisheries Science Center's West Coast groundfish bottom trawl survey, either because of the inability of the survey to sample rocky habitat with trawl gear or because of other restrictions on sampling locations. Because these species are not well sampled, the majority of historical information (e.g., length and age data) available for assessment comes primarily from recreational and commercial fishery samples. Yet, because of restrictions on retention of fish triggered by rebuilding plans, often, recreational and commercial fishery behavior has been profoundly altered (Stewart et al.[2]). In the most recent assessment of yelloweye rockfish, limited fishery data during rebuilding were cited as a challenge to "produce conclusive information about the stock for the foreseeable future" (Stewart et al.[2]). Another overfished rockfish species, cowcod, was assessed most recently by using a data-moderate approach that did not include length or age data instead of the historical data-rich integrated assessment because of lack of data during the rebuilding period. Often fishermen avoid targeting stocks during rebuilding efforts for rockfish species even as harvest limits increase with rebuilding populations and this precaution results in harvests that are well below the rebuilding harvest limits and in continued low levels of biological samples from the fishery catch. Additionally, harvest restrictions can affect the harvest of more abundant fish stocks that co-occur with rebuilding stocks and can result in reduced data availability that extends beyond a single species.

Despite a limited harvest of a stock, continued data collection is necessary to determine the extent to which that stock has rebuilt. The ability to measure the rate of recovery is crucial for management, and increased uncertainty due to limited data can impede the determination of whether a stock is on track to rebuild in a specified time frame. Additionally, biological data are critical for improvement of estimates of key parameters within stock assessments (e.g., natural mortality; growth; recruitment compensation, which is termed *steepness*) and can indicate incoming poor or strong recruitment year classes that will affect estimates of relative stock biomass (the ratio of current biomass to unfished biomass) and rebuilding rates. Potential improvements in parameter estimates and the ability to detect incoming fluctuations in recruitment during rebuilding are restricted when collection

tus and productivity of Cowcod, *Sebastes levis*, in the Southern California Bight, 2013, 166 p. Fish Ecol. Div., Southwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, Santa Cruz, CA. [Available from website.]

[4] Thorson, J. T., and C. Wetzel. 2016. The status of canary rockfish (*Sebastes pinniger*) in the California Current in 2015, 241 p. Northwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, WA. [Available from website.]

[5] Hamel, O. S., and K. Ono. 2011. Stock assessment of Pacific ocean perch in waters off of the U.S. West Coast in 2011, 135 p. Pacific Fishery Management Council, Portland, OR. [Available from website.]

of new biological data is severely limited because of harvest restrictions.

An understanding of the long-term effect of reduced data on the ability to monitor a stock during rebuilding would provide insight and guidance for management. Numerous simulation studies have evaluated the impact of data quality and quantity on the performance of stock assessment methods (e.g., Hilborn, 1979; Chen et al., 2003; Yin and Sampson, 2004; Magnusson and Hilborn, 2007; Wetzel and Punt, 2011; Lee et al., 2012); however, studies often focus on the ability to estimate either management quantities or biological parameters. The simulation performed in our study evaluated the ability to accurately monitor rebuilding of an overfished, long-lived rockfish stock for which harvest and the collection of fishery data are restricted during rebuilding. This simulation study addressed 3 main questions: 1) Do limited data result in increased uncertainty that affects the ability to detect when an overfished stock has rebuilt, 2) Can limited data from the fishery be used to detect a shift in fishery selectivity that results from changing fishing behavior during rebuilding, and 3) How are model estimates of stock size and biological parameters affected during periods of limited data?

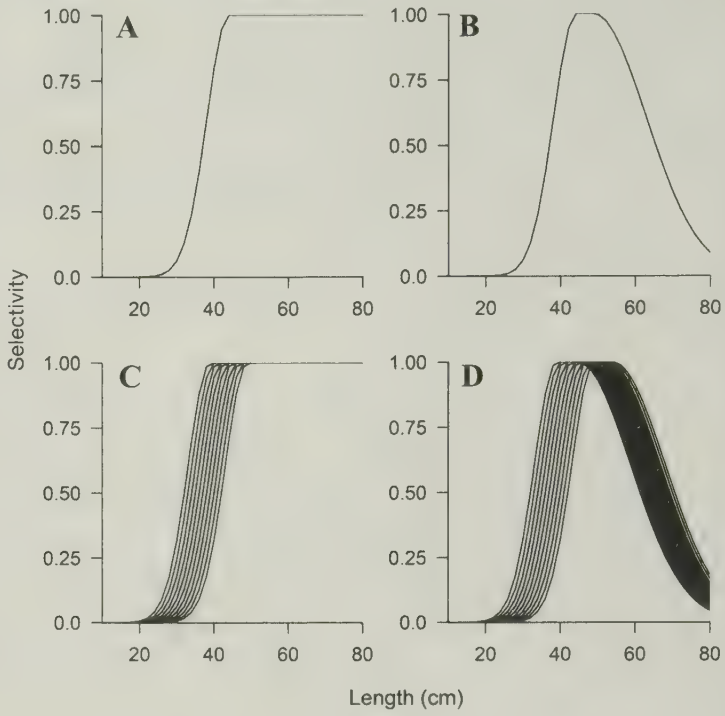

Figure 1

Fishery selectivity for the time-invariant case during (**A**) the historical and rebuilt periods and (**B**) the overfished period and for the time-varying case during the (**C**) historical and rebuilt periods and the (**D**) overfished period. These 2 alternative cases were used in the operating model to account for the potential effects of time-varying natural mortality and fishery selectivity on simulated rockfish stocks. A standard error of 0.05 was applied annually for size at maximum selectivity, which defined the variability of the ascending limb of the selectivity curve (in panels C and D, and a standard error of 0.20 was applied for the width at maximum selectivity that defined the length at which the dome in selectivity began while the stock was estimated to be overfished (in panel D) (for additional details on double normal selectivity, see Methot and Wetzel, 2013).

Materials and methods

General approach

A rockfish life-history type common to the U.S. west coast was simulated (Table 1). West coast rockfish species are assumed to have a range of natural mortality and productivity levels, from long-lived and slow growing (e.g., yelloweye rockfish) to medium-lived and intermediate-growing life histories (e.g., black rockfish [*Sebastes melanops*]). The operating model was parameterized by using intermediate natural mortality and steepness values to represent the general life-history dynamics of a U.S. west coast rockfish species.

Two alternative cases were simulated by using the operating model to account for the potential impacts of time-varying natural mortality and fishery selectivity. The first case, referred to as *time-invariant*, involved a single fixed rate of natural mortality over the entire time period. The fishery selectivity was assumed (and fixed) to be asymptotic during the historical period, dome-shaped during the overfished period, and then again asymptotic after the simulated stock was rebuilt (Fig. 1, A and B). The simulated stocks were reduced to an overfished state (below MSST) at the time of the first assessment in year 50. The shift in selectivity during the period in which the simulated stock was estimated to be overfished was designed to represent potential changes in fishing behavior that result from harvest restrictions that could affect the estimation performance, if not detected because of lack of data to inform the model about the shape of fishery selectivity.

The second case, referred to as *time-varying*, involved annual deviations in natural mortality and in the parameters on which the fishery selectivity pattern was based during the historical, overfished, and rebuilt periods (Fig. 1, C and D). All time-varying parameters were designed to produce data that would be less informative about either the biology or the fishery behavior and to better emulate the complexity of real fishery data. Annual deviations in fishery selectivity were applied to 2 selectivity parameters: 1) the length bin (in centimeters) at which the as-

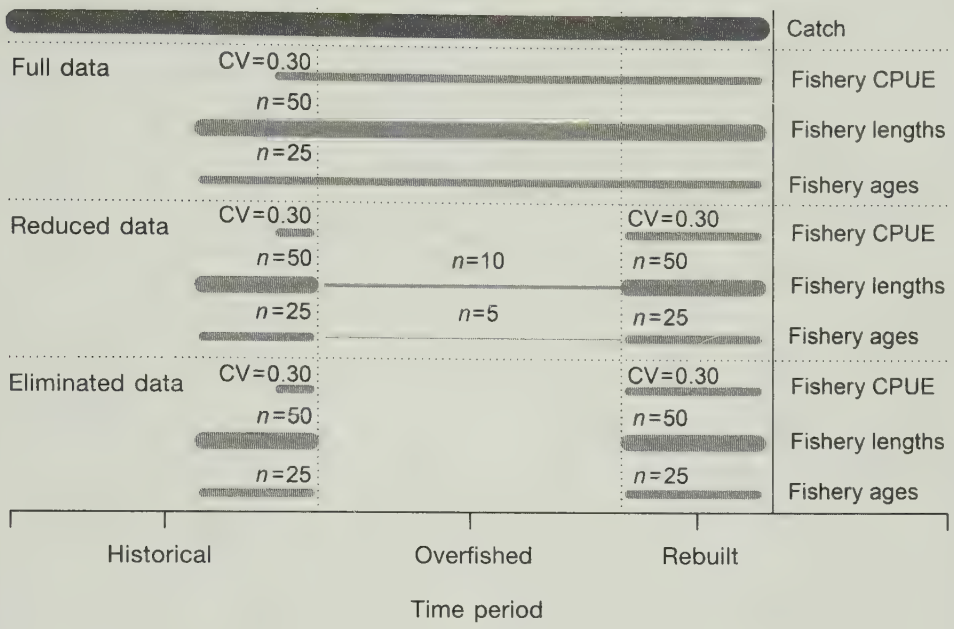

Figure 2

Summary of the data available for each of the 3 data scenarios (full data, reduced data, and eliminated data) created to explore the impact of data availability on the ability to monitor rebuilding of an overfished stock of rockfish species: coefficient of variation (CV) and number of samples (n) for catch per unit of effort (CPUE), lengths, and ages from the fishery. Historical length and age data from the fishery begin in year 35, 15 years before the first assessment, and the fishery CPUE data start in year 45. The management period begins in year 50 when data quantity and quality change by data scenario. Data quantity and quality return to historical levels when the simulated stock has been estimated to be rebuilt to the target biomass. Thickness of the horizontal lines reflects the different sample sizes; all fishery data are shown in dark gray and catches are shown in black. Catches were known without error and were available for all data scenarios.

cending limb of selectivity curve reached maximum selectivity (termed *size at maximum selectivity*, Fig. 1C, Fig. 2) the width of the plateau for the maximum selectivity (defined as a logistic function between the peak and the maximum length bin) that results in a dome-shaped selectivity curve (termed *width at maximum selectivity*, Fig. 1D) during the years the simulated stock was overfished. A standard error of 0.05 was applied annually for the size at maximum selectivity parameter for all years, and a standard error of 0.20 was applied for the width at maximum selectivity parameter during the years the simulated stock was estimated to be overfished. The level of variation for each parameter was selected to ensure that the ascending limb of the selectivity curve was greater than the length at 50% maturity (37 cm) within the operating model and that the width of maximum selectivity (the parameter that creates the dome-shaped curve) was small enough to allow potential detection by the estimation method (a portion of the population with reduced selectivity that is detected because of a dome-shaped curve). Additionally, autocorrelated annual deviations in natural mortality were applied to the population within the operating model.

The operating model was a single-sex, age-structured model in which an annual index of fishery catch per unit of effort (CPUE) was observed with error and in which length- and age-composition data were collected for select years. These data were used by the estimation method to estimate population size and a catch level. The catches were removed without error from the simulated stock. Data generation, catch estimation, and simulated stock updating were conducted in an iterative fashion for 100 years (termed the *management period*), a length of time that would allow the simulated stock to recover to at least the target biomass.

The operating model

The numbers-at-age at the start of the year are computed with the following equation:

$$N_{t+1,a}=\begin{cases} R_t & \text{if } a=0 \\ N_{t,a-1}e^{-(M_t+S_{t,a-1}F_t)} & \text{if } 1\le a<A-1, \\ N_{t,A-1}e^{-(M_t+S_{t,A-1}F_t)}+N_{t,A-1}e^{-(M_t+S_{t,A}F_t)} & \text{if } a=A \end{cases} \quad (1)$$

where $N_{t,a}$ = the number of fish of age at the start of the year t;
R_t = the number of age-0 fish at the start of year t;
$S_{t,a}$ = the selectivity during year t for fish of age a;
A = the plus group (i.e., the oldest age group modeled, set equal to age 70);
F_t = the instantaneous fishing mortality rate during year t; and
M_t = the instantaneous rate of natural mortality during year t.

Natural mortality for year is defined as

$$M_t = Me^{-0.5\sigma_M^2+\varepsilon_t^M}, \quad (2)$$

where M = the mean value of natural mortality;
σ_M = the standard error of the annual deviations in natural mortality; and
ε_t^M = the autocorrelated lognormal deviation in natural mortality for year t:

$$\varepsilon_t^M = \rho\varepsilon_{t-1}^M + \sqrt{1-\rho^2}\phi_t \quad \phi_t \sim N(0;\sigma_M^2), \quad (3)$$

where ρ = the level of autocorrelation associated with natural mortality; and
ϕ_t = the deviation in natural mortality for year t. The time-invariant natural mortality case assumed $\sigma_M=0$ and hence $\varepsilon_t^M=0$.

The number of age-0 fish is related to spawning biomass according to the Beverton–Holt stock recruitment relationship (Beverton and Holt, 1957):

$$R_t = \frac{4hR_0SB_t}{SB_0(1-h)+SB_t(5h-1)}e^{-0.5\sigma_R^2+\varepsilon_t^R} \quad \varepsilon_t^R \sim N(0;\sigma_R^2), \quad (4)$$

where R_0 = the number of age-0 fish when the population is in an unfished state;
SB_0 = the unfished spawning biomass;
SB_t = the spawning biomass at the start of the spawning season in year t;
σ_R = the standard deviation of recruitment in log space; and
h = steepness.

A nonequilibrium starting condition was created by applying the numbers-at-age (combined with the natural mortality calculations for the number of years equal to the maximum age before the start of fishing) with variation in recruitment from the Beverton–Holt stock recruitment relationship. Historical catches for years 1–50 were generated so that the populations were at $0.15SB_0$ in year 50, a state that would allow correct detection by the estimation method that the simulated stocks were in an overfished state. Additionally, the simulated populations would require an extended number of years for the simulated stock to rebuild to the target biomass when a period of reduced data could affect the performance of the estimation method to correctly estimate the stock size and status. The catch of fish of age a during year t in numbers was given by

$$C_{t,a} = \frac{S_{t,a}F_t}{M_t+S_{t,a}F_t}N_{t,a}(1-e^{-M_t-S_{t,a}F_t}). \quad (5)$$

The observation model was used to generate a fishery CPUE index for each year t:

$$I_t = QB_te^{-0.5\sigma_f^2+\varepsilon_t^f} \quad \varepsilon_t^f \sim N(0;\sigma_f^2), \quad (6)$$

where Q = the catchability coefficient;
σ_f = the standard deviation of catchability in log space; and
B_t = the vulnerable biomass available to the fishery in the middle of year t:

$$B_t = \Sigma_{a=1}^{A} w_a S_{t,a} N_{t,a} e^{-0.5(M_t+S_{t,a}F_t)}, \quad (7)$$

where w_a = the weight of a fish of age a.

The length- and age-composition data for the fishery were assumed to be multinomially distributed (for details, see the "Data scenarios" section). Age-determination error was assumed to be normally distributed with ages subject to a 5% standard deviation by age.

The fishery selectivity was modeled by using the double normal parameterization (for details, see Methot and Wetzel, 2013), which is a flexible form that allows selectivity to range in shape from asymptotic to dome-shaped. Fishery selectivity during the historical period (years 1–50) was assumed to be asymptotic (Fig. 1, A and C). Fishery selectivity shifted to a dome-shaped (in contrast with the historical asymptotic) form (Fig. 1, B and D) within the operating model during the period that the simulated stock was estimated to be below the target biomass ($0.40\ SB_0$). Once the population was estimated to have recovered to above the target biomass, fishery selectivity reverted to the asymptotic form. The shift in selectivity was designed as a way to mimic a change in the behavior of fishermen that results from an overfished designation (e.g., 1) the creation of rockfish conservation areas that protect portions of the stock, or 2) areas of known specific habitat that are avoided by fishermen, or 3) areas associated with high abundance of the overfished stock). The change in shape of the selectivity curve depended on the estimated stock status rather than on the true status from the operating model (i.e., changes in behavior of fishermen modeled by a change in selectivity were assumed to be driven by management restrictions based on the perception of the simulated stock by the estimation method rather than on the true unobservable state of the simulated stock).

The estimation method

Stock synthesis, an integrated statistical catch-at-age model (Methot and Wetzel, 2013), was the estimation

method used to assess the simulated stocks. Stock synthesis was applied for the first time in year 50 and then every 6th year thereafter. Assessment frequency for U.S. west coast groundfish species varies as a consequence of commercial importance (an indicator of exploitation), the time since last assessment, and life history dynamics of the stock (Methot, 2015). Long-lived rockfish species generally have slow dynamics, resulting in minimal fluctuations in biomass from year to year (assuming non-extreme harvesting). To mimic the likely cycle of assessments for this type of stock in real life, we conducted the assessment every 6th year.

Parameters determining unfished recruitment (R_0), steepness, growth, annual recruitment deviations, initial age-structure deviations, and the size and width at maximum selectivity for the fishery selectivity that assumed a double normal parameterization (same as assumed in the operating model). Steepness was estimated by using a diffuse beta prior within the estimation method. All other parameters were estimated without priors. Natural mortality, the variation of length-at-age, weight-at-length, the fecundity relationship, and the variation of recruitment (σ_R) were assumed known. The ratio of spawning biomass to unfished spawning biomass (termed *relative spawning biomass*) in the assessment year was estimated and the forecasted catches were determined by using the harvest control rule adopted by the Pacific Fishery Management Council (PFMC) for rockfish species. The catches were removed from the operating population without error, and then the fishery CPUE index and length- and age-composition data were generated for the subsequent 6 years.

The harvest control rule adopted by the PMFC for rockfish species involves a linear reduction in catch when a stock falls below $0.40SB_0$, and no fishing when the stock falls below $0.10SB_0$. The maximum catch, termed the *overfishing level catch* was defined as the catch corresponding to the proxy for the fishing mortality rate at which maximum sustainable yield is achieved and if surpassed would constitute overfishing, was set equal to the target harvest rate measured as spawning biomass per recruit ($F_{0.50}$) multiplied by SB_t. Spawning biomass per recruit is a measure of fishing mortality on the projected average contribution of each recruit to the spawning biomass. Applying an $F_{0.50}$ harvest rate reduces the spawning biomass per recruit to 50% of the unfished condition. The catch predicted by the overfishing level was reduced by a management buffer to determine the acceptable biological catch level (i.e., the default reduction for the PMFC for an age-structured assessment sets the acceptable biological catch equal to 95.6% of the overfishing level catch, Ralston et al., 2011). The annual catch limit was set equal to the acceptable biological catch when the simulated stock was above the target biomass, $0.40SB_0$, or reduced from the acceptable biological catch according to the harvest control rule when the simulated stock fell below $0.40SB_0$.

One major simplification in this simulation design was the omission of the rebuilding plans that are implemented when a stock is assessed to have fallen below the MSST (defined as $0.25SB_0$ for U.S. west coast rockfish species). In reality, harvest for stocks that fall below the MSST is not based on the standard harvest control rule but rather on a rebuilding plan in which catches are determined until the stock is rebuilt to the target biomass (for additional details on PFMC rebuilding plans, see Wetzel and Punt, 2016).

Data scenarios

Three data scenarios were created to explore the impact of data availability on the ability to monitor rebuilding of an overfished stock (Fig. 2). The data scenarios were designed to emulate a stock, similar to many rockfish species off the U.S. west coast, that is infrequently encountered by a fishery-independent survey (e.g., because of depth or habitat) and for which only fishery data were available. The sample sizes of the historical length and age data generally were based on the effective sample sizes observed for yelloweye rockfish. Historical length and age data from the fishery begins in year 35, 15 years before the first assessment, and the fishery CPUE data starts in year 45. Following the first assessment in year 50, the 3 scenarios have different data availability based on estimated stock status (e.g., overfished versus rebuilt) in the assessment year.

The *full data* scenario maintained the fishery CPUE index and length- and age-composition data at the historical levels (before the stock being declared overfished in year 50) during rebuilding (Fig. 2). The *reduced data* scenario decreased the amount of data available from the fishery during rebuilding (Fig. 2). The length- and age-composition data were reduced to 20% of the historical sample sizes during rebuilding and the fishery CPUE index was eliminated during the rebuilding period. When the simulated stock was estimated to have rebuilt to the target biomass, the CPUE index resumed and the sample sizes of composition data reverted to historical levels. The *eliminated data* scenario had no fishery data during rebuilding (Fig. 2). The fishery CPUE index and composition data resumed at historical sample sizes when the simulated stock was projected to be rebuilt.

The estimation method in the full and reduced data scenarios was allowed to estimate a change in selectivity from asymptotic to dome-shaped during the rebuilding period through the application of a time block on selectivity. However, the eliminated data scenario assumed constant asymptotic selectivity in the assessment for all years because no fishery composition data were available to detect a potential shift in selectivity. In reality, input from fishermen may be used to justify an updating of the selectivity form. Methods that have been used for stocks off the U.S. west coast have applied a default assumption for asymptotic selectivity in assessments that do not incorporate composition data. Incorrectly assuming dome-shaped selectivity when the true form is asymptotic could result in overly optimistic estimates of the population status because dome-

shaped selectivity means that there are older individuals in the population that are not subject to fishing pressure. The eliminated data scenario assumes what might be considered a more precautionary assumption for selectivity in the absence of composition data.

Sensitivity to adding survey data

Additional simulations were conducted to evaluate the impact of having only fishery information versus indices of abundance and length- and age-composition data available from both a fishery-independent survey and a fishery. The operating model generated a highly uncertain survey (coefficient of variation: 0.40) that was conducted on a biennial basis with low sample sizes (n=10 per year) for length- and age-composition data starting in year 40, 10 years before the first assessment in year 50. The survey selectivity was assumed to be fixed at an asymptotic shape, selecting fish at smaller sizes in relation to the fishery selectivity. All other specifications for the fishery within the operating model and the assumptions applied by the estimation method were the same as those detailed previously.

Performance measures

The outcomes of the simulations for each case and data scenario were summarized by using 5 metrics that were selected to evaluate the effect of data on estimation of indicators of stock status (e.g., relative spawning biomass) and management quantities (e.g., rebuilding catch).

1 The relative errors (REs) for estimated parameters, calculated as

$$RE = \frac{E - T}{T}, \quad (8)$$

where E = the estimated quantity of interest; and
T = the true value from the operating model.
The REs for spawning biomass and relative spawning biomass were calculated for each simulation for the ending year estimate each time the simulated stock was assessed.

2 The percent root mean square error (RMSE), a measure of precision and bias, was calculated to assess the overall level of error given the amount of data available:

$$RMSE = \sqrt{\frac{1}{n}\Sigma_{i=1}^{n}\frac{(E_i - T_i)^2}{T_i^2}}, \quad (9)$$

where n is the number of simulations (n=100).

3 The average (over simulations) of the total catch while the simulated stock was recovering to the target biomass.

4 The annual average variability of the catches (AAV), defined as

$$AAV = 100\frac{\Sigma_t|C_t - C_{t+1}|}{\Sigma_t C_t}, \quad (10)$$

where C_t = the catch during year t.

5 The percentage of simulations with stocks that rebuilt to the target biomass and percentage of simulations with stocks that remained overfished at the end of the management period.

Results

Assessment performance with time-invariant parameters

The full and reduced data scenarios performed similarly while simulated stocks were rebuilding and after stocks had rebuilt, and the trends of the relative error for spawning biomass and relative spawning biomass were generally consistent between the full and reduced data scenarios (Fig. 3, A, B, D, and E). The median estimates of spawning biomass and relative spawning biomass were less than the true values during rebuilding for both scenarios (Fig. 3, A, B, D, and E). As expected, the full data scenario had less among-simulation variability in the differences in spawning biomass and relative spawning biomass between the operating model and estimation method during the rebuilding period than the variability in the reduced and eliminated data scenarios (Fig. 3, A–F). However, the among-simulation variability of errors in biomass metrics was similar between the full and reduced data scenarios by the end of the management period, when a majority of the simulated stocks were estimated to be rebuilt and data collections had returned to historical, higher sample sizes for the reduced data scenario.

The eliminated data scenario in which no data were available during the rebuilding period resulted in median (across simulations) estimates of spawning biomass and relative spawning biomass errors that were similar to the true values but were highly imprecise at the start of the management period (years 50–74) (Fig. 3, C and F). The eliminated data scenario, in the absence of new data during rebuilding, projected the simulated stocks on the basis of the historical data and new catches until the simulated stock was rebuilt, at which time data collection resumed and allowed the estimation method to estimate population status. The median estimates of spawning biomass and relative spawning biomass for the eliminated data scenario were less than the true values, and had high among-simulation variability in error as simulated stocks began to be projected to be rebuilt and data collection resumed. In contrast to the full and reduced data scenarios, the estimates of spawning biomass and the relative spawning biomass for the eliminated data scenario had little improvement in the among-simulation variability in error estimates by the end of the management period (Fig. 3, C and F).

Even when data collection continued at reduced levels in the reduced data scenario, the estimates of steepness varied in relation to the steepness estimates from the full data scenario. The full data scenario resulted in generally median unbiased estimates during the rebuilding period and small positive median bias by

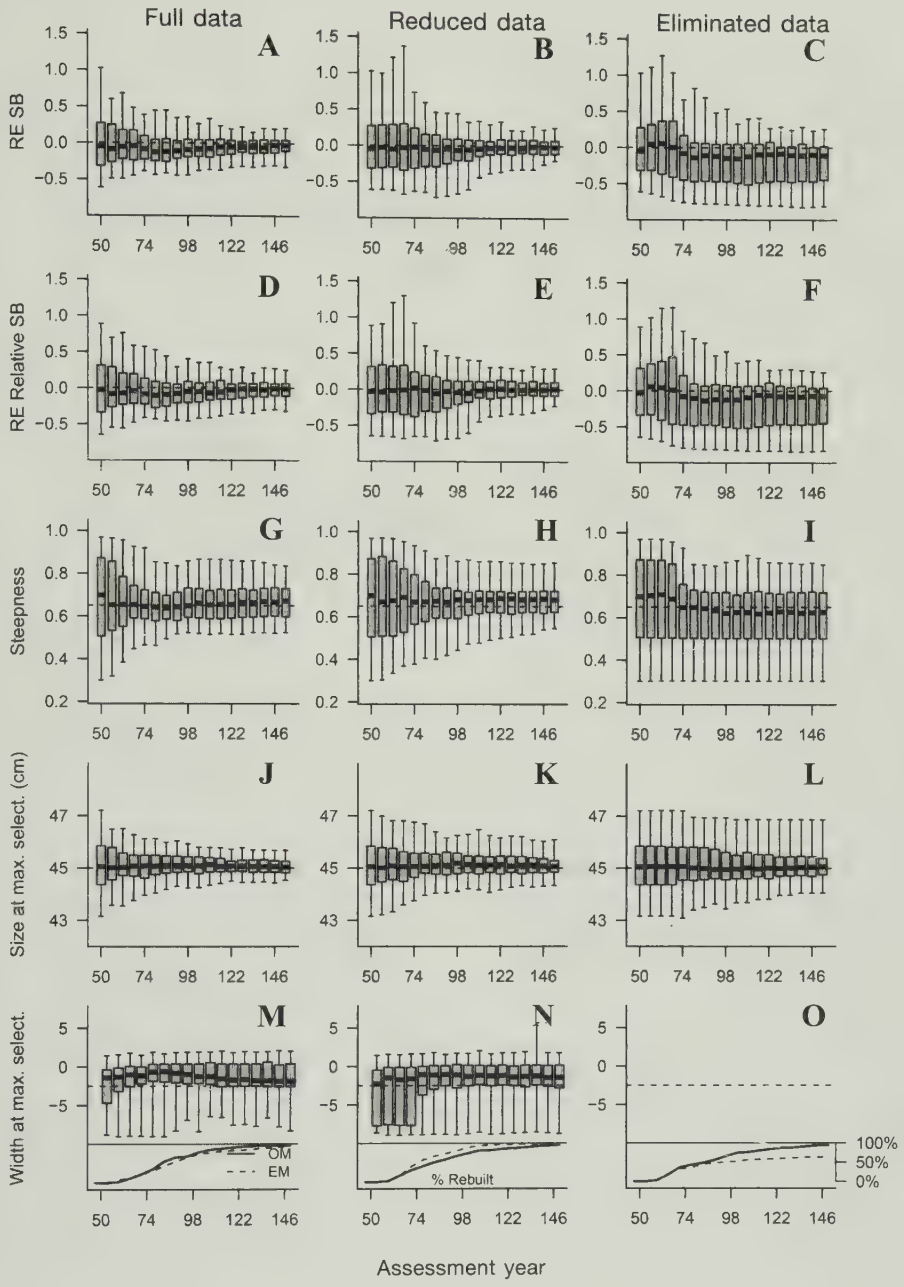

Figure 3

Relative error (RE) of estimated spawning biomass (SB) and relative SB, estimates of steepness, size at maximum selectivity, and the width at maximum selectivity in each assessment year for the time-invariant case and all 3 data scenarios (full data, reduced data, and eliminated data) for all simulations used to examine the effect of data availability on the ability to monitor rebuilding of an overfished stock of a rockfish species. The eliminated data scenario in the absence of composition data had selectivity fixed at the asymptotic assumption and hence did not estimate the width at maximum selectivity parameter. The percentage of stocks that had rebuilt to the target biomass during the management period (shown in bottom panels) within the operating model (OM, solid black line) and the estimation method (EM, dashed black line); data collection consequently returned to historical levels when the EM determined that the stock was rebuilt. The black lines in the gray boxes denote the median of the estimates, the gray boxes cover the 25–75% simulation interval, and the boxplot whiskers indicate the 95% simulation interval for each assessment year.

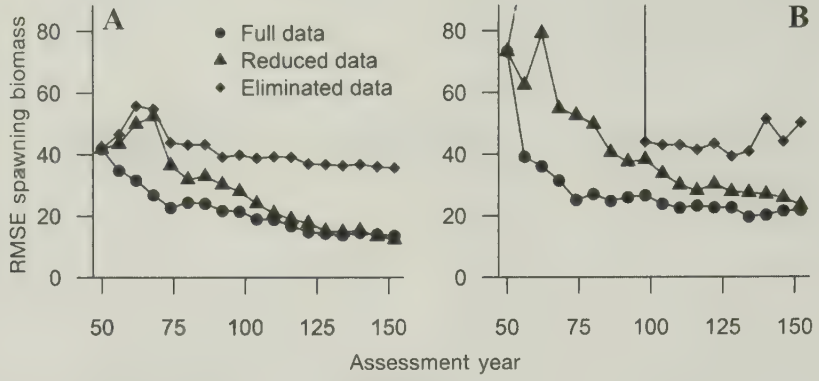

Figure 4

The root mean square error (RMSE) for spawning biomass (SB) by assessment year for each case, (**A**) time invariant and (**B**) time varying, and for each data scenario (full data, reduced data, eliminated data). The scale of the y-axis is the same for comparability of results between the time-invariant and the time-varying simulations. The time-varying eliminated data scenario peaked in year 68 at 221% RMSE.

the end of the management period (Fig. 3G; note that the term *median unbiased* is used to define cases in which the median of the relative errors equals zero). In contrast, the median of the estimates of steepness for the reduced data scenario were greater than the true steepness during the management period (Fig. 3H). The eliminated data scenario had the highest among-simulation variability among estimates of steepness during the management period (Fig. 3I) as a result of the mixture of simulations in which stocks had rebuilt and not rebuilt.

Reduction or elimination of data during rebuilding increased the among-simulation variability in estimates of the size at maximum fishery selectivity and the median estimates were generally equal to the true value for all data scenarios (Fig. 3, J–L). The among-simulation variability of the estimates for the reduced and eliminated scenarios improved when the majority of the simulated stocks were estimated to be rebuilt and fishery composition sample sizes returned to historical levels. The full and reduced data scenarios were allowed to estimate dome-shaped selectivity during the rebuilding period and resulted in median estimates of the width at maximum selectivity that exceeded the true values and were highly variable among simulations at the start of the management period (Fig. 3, M and N). The eliminated data scenario did not allow estimation of dome-shaped selectivity because of the absence of fishery composition data. The estimates from the full and reduced data scenarios for the width at maximum selectivity that exceeded the true values for this parameter indicated that the data available were not sufficient to inform the estimation method about the severity of the dome shape in the selectivity curve during rebuilding. A higher estimated value indicates that the dome in selectivity occurs at larger sizes with a higher proportion of the population in relation to the operating model at full selectivity. The full data scenario resulted in markedly improved estimates of the shape of the dome over the management period, compared with estimates in the reduced data scenario (Fig. 3, M and N).

The RMSE for the estimated spawning biomass for each assessment year shows the increased precision of the full data scenario during the rebuilding period compared with that of the reduced and eliminated data scenarios (Fig. 4A). The eliminated data scenario resulted in the highest RMSE over the entire management period (Fig. 4A). However, the RMSE for the reduced data scenario improved over the management period as simulated stocks began to be assessed as rebuilt to the target biomass and as sample sizes returned to historical levels. The limited improvement in the RMSE for the eliminated data scenario was driven by the simulations in which the stocks never were projected to rebuild to the target biomass (35 out of 100 simulations).

In the absence of data collection, the performance of the estimation method was dependent upon the ability of the historical data to inform parameter estimates. An examination of the eliminated data scenario more closely revealed a pattern in the performance of the estimation method based on the estimation of steepness in the first assessment year. The eliminated data scenario simulations were divided and plotted on the basis of whether the estimation method projected the stock in the simulation to rebuild (65 simulations) or to fail to rebuild (35 simulations) by the end of the management period. To allow comparison between the eliminated and the full data scenarios, the estimates from the full data scenario were also divided into the same 2 groups and plotted. The estimates of spawning

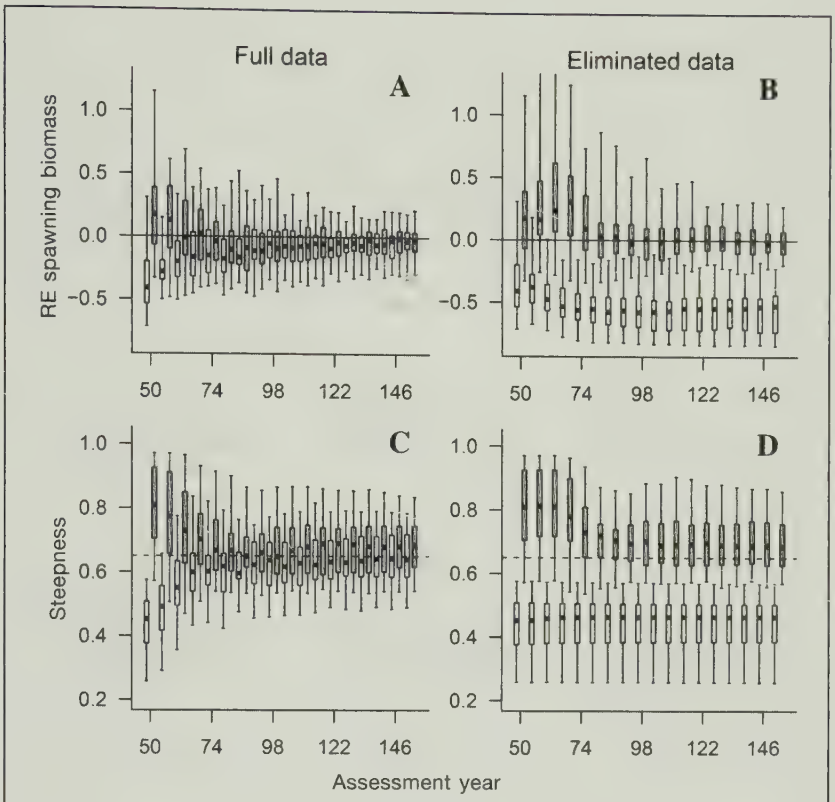

Figure 5

Relative error (RE) of spawning biomass and the estimates of steepness for the full and eliminated data scenarios for the time-invariant case; results are divided by whether the simulated stock was estimated to be rebuilt (65 simulations [gray]) or not (35 simulations [white]) for the eliminated data scenario. The black lines in the gray boxes denote the median of the estimates, the gray boxes cover the 25–75% simulation interval, and the boxplot whiskers indicate the 95% simulation interval for each assessment year.

biomass were considerably less than the true values in the first assessment year (Fig. 5B) for the 35 simulations in which the stocks were estimated not to rebuild by the end of the management period. The underestimates of spawning biomass (Fig. 5B) were driven by estimates of steepness that were much less than the true value in the first assessment (Fig. 5D). In the absence of new data, the underestimates of steepness resulted in the estimation method perceiving a less productive stock that required an extended period to rebuild to the target biomass. However, with full data present, estimated quantities (spawning biomass and steepness) improved for this subset of simulations and were median unbiased by the end of the management period (Fig. 5, A and C).

The median number of years estimated for the simulated stocks to recover to the target biomass for the full data scenario was longer than the median time required to rebuild the stock within the operating model simulations (Table 2). In contrast, both the reduced and eliminated data scenarios had shorter median recovery times than those of the operating model (Table 2). The contrast in estimated recovery times across the data scenarios was related to the average catch obtained during rebuilding along with the bias and variability of estimates. The median error associated with relative spawning biomass for the full data scenario was less than zero, and there was low among-simulation variability (compared with those of the other data scenarios) for all assessment years, which resulted in estimates that predicted constant rebuilding but at a slower rate than the true rate of the simulated stock in the operating model (Fig. 3D). In contrast, the reduced data scenario had higher variability over time (i.e., within-simulation) across the estimates of error associated with relative spawning biomass (Fig. 3E). The variability of estimates between assessments resulted in simulated stocks that were estimated to be recovered to the target stock size when the populations in the operating model were not yet recovered because of estimation error driven by the limited number of composition samples during rebuilding.

Table 2

The median and 90% simulation interval (SI) for the estimated number of years needed for simulated rockfish stocks to rebuild to the target biomass, the operating model number of years needed for the stocks to rebuild to target biomass, and the number of stocks that failed to rebuild to the target biomass determined by the estimation method (EM) and the operating model (OM) for each case and data scenario.

Selectivity/data scenario	Estimated number of rebuilding years		Operating model number of rebuilding years		Number of stocks that failed to rebuild	
	Median	90% SI	Median	90% SI	EM	OM
Time-invariant						
Full data	43	(13–87)	34	(16–73)	7	4
Reduced data	31	(19–61)	34	(14–83)	1	5
Eliminated data	25	(14–72)	37	(14–87)	35	4
Time-varying						
Full data	31	(13–91)	35	(13–85)	13	4
Reduced data	25	(13–79)	32	(12–74)	8	2
Eliminated data	25	(13–77)	36	(12–79)	32	5

Table 3

The median and 90% simulation intervals (SI) for the average catch of simulated rockfish stocks during rebuilding, the annual average variability of the catches (AAV) during rebuilding, and the AAV over all years for each case and data scenario.

Selectivity and data scenario	Average catch during rebuilding		AAV during rebuilding		AAV all years	
	Median	90% SI	Median	90% SI	Median	90% SI
Time-invariant						
full data	44.0	(15.3–78.9)	6.0	(3.7–11.5)	3.2	(2.1–4.7)
reduced data	28.1	(14.6–57.9)	7.7	(4.0–14.5)	3.5	(2.3–5.3)
eliminated data	41.3	(19.9–83.8)	2.6	(1.3–4.4)	2.2	(1.3–3.9)
Time-varying						
full data	31.7	(11.0–75.4)	7.3	(4.4–17.5)	4.2	(2.7–5.9)
reduced data	25.1	(15.6–68.0)	8.9	(4.5–20.7)	4.5	(2.6–9.8)
eliminated data	36.3	(15.7–79.4)	2.3	(1.2–4.8)	2.8	(1.3–5.3)

The reduced data scenario had the lowest median average catch during rebuilding (Table 3), and the median rebuilding time was estimated to be shorter than the true time to recovery within the operating model (Table 2). The eliminated data scenario, which was entirely dependent upon historical data until the simulated stocks were projected to rebuild, essentially projected the population forward with each assessment on the basis of the initial parameter estimates from the historical data and resulted in high median average catches during rebuilding and the lowest median AAV during rebuilding and across the entire management period (Table 3).

The effect of time-varying parameters

Time-varying annual deviations in natural mortality and fishery selectivity generally resulted in increased among-simulation variation in estimation errors than with the time-invariant case. The median error of estimates of spawning biomass at the time of the first assessment exceeded the true values and were highly variable among simulations (Fig. 6, A–C). The among-simulation variance in errors of estimates of spawning biomass decreased markedly for the full data scenario after the first assessment (Fig. 6A). However, this variability remained high for approximately the first 25 years of the management period (assessments were performed every fourth year between years 50–74 approximately) for both the reduced and eliminated data scenarios, until approximately 50% of the simulated stocks were estimated to be recovered and the fishery sample sizes increased to historical levels (Fig. 6, B and C). The full and reduced data scenarios resulted in median spawning biomass estimates that were generally smaller than the operating model values (Fig. 6, A and B). However, the medians of the errors for relative spawning biomasses were variable over the manage-

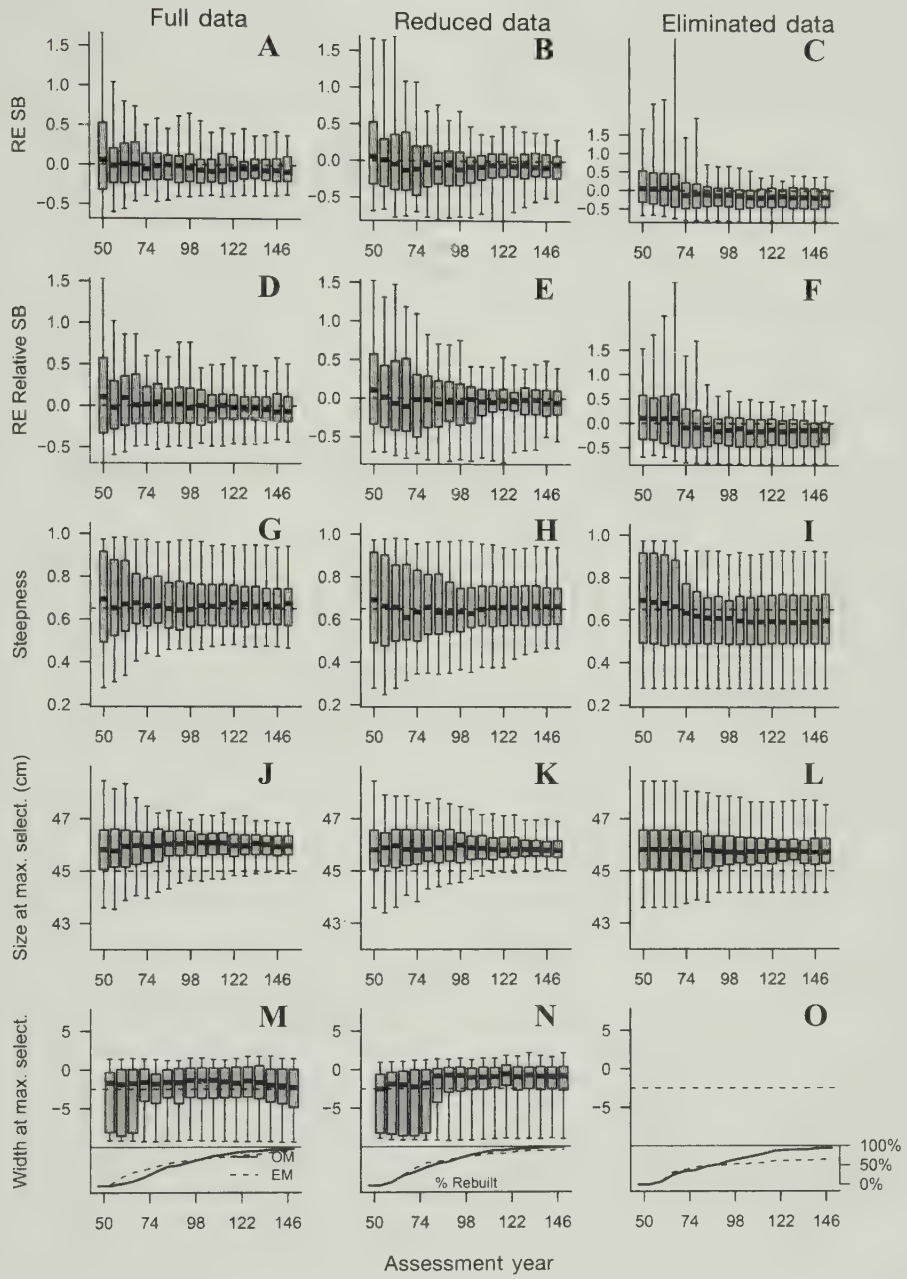

Figure 6

Relative error (RE) of estimated spawning biomass (SB) and relative SB, estimates of steepness, size at maximum selectivity, and the width of at maximum selectivity in each assessment year for the time-varying case and all 3 data scenarios (full data, reduced data, and eliminated data) for all simulations used to examine the effect of data availability on the ability to monitor rebuilding of an overfished stock of rockfish species. The eliminated data scenario in the absence of composition data had selectivity fixed at the asymptotic assumption and hence did not estimate the width at maximum selectivity parameter. The percentage of stocks that had rebuilt to the target biomass during the management period within the operating model (OM, solid black line) and with the estimation method (EM, dashed black line) is shown in the bottom panels. Data collection consequently returned to historical levels when the EM determined that the stock was rebuilt. The black lines in the gray boxes denote the median of the estimates, the gray boxes cover the 25–75% simulation interval, and the boxplot whiskers cover the 95% simulation interval for each assessment year

ment period (Fig. 6, D and E). The medians of the estimates of relative spawning biomass for the eliminated data scenario were larger than operating model values at the start of the management period but became smaller than the values as simulated stocks rebuilt to target biomass levels and data collection resumed (Fig. 6F).

Inclusion of time-varying selectivity resulted in the median estimates of the size at maximum selectivity (the earliest size at which selectivity reaches a maximum value) across all data scenarios exceeding the mean of the operating model values (Fig. 6, J–L), although the full data scenario resulted in the lowest among-simulation variation. The full and reduced data scenarios, which were allowed to estimate dome-shaped selectivity (width at maximum selectivity) during the recovery period, resulted in highly variable among-simulation estimates at the start of the management period and the variability for the estimates decreased earlier for the full data scenario (Fig. 6, M and N).

Compared with the case with time-invariant parameters, the RMSE was higher for all data scenarios when time-varying parameters were present within the operating model (Fig. 4). The RMSE for the estimated spawning biomass for the full data scenario was lower than that of the other scenarios for the entire management period (Fig. 4B). Similar to the time-invariant results, the RMSE of spawning biomass for the eliminated data scenario was the highest between the scenarios across the entire management period, peaking in assessment year 68 at 221% (a single simulation for the eliminated data scenario, with extreme outliers for 2 assessment years, was removed for a more informative summary of the RMSE).

The time-varying results for the eliminated data scenario were qualitatively similar to those for the time-invariant case, in which stocks were not projected by the estimation method to be rebuilt for a large number of simulations (32 simulations). As was observed in the time-invariant case, the simulations with time-varying parameters and stocks projected to fail to rebuild biomass had median estimates of spawning biomass and relative spawning biomass below the operating model values at the time of the first assessment, which were driven by estimates of steepness that were considerably lower than the true value (not shown).

The inclusion of time-varying parameters in the operating model resulted in shorter median estimated recovery times in relation to the time-invariant case for the full and reduced data scenarios (Table 2). However, the median number of years to rebuild for stocks in the operating model were similar between the time-varying and time-invariant cases. The estimation method produced earlier recovery times for the time-varying case because of the increased variability in the estimates of relative spawning biomass and resulted in the estimation method having an increased frequency of erroneous estimation of the biomass to be above the target stock size (Fig. 3, D–F, versus Fig. 6, D–F).

The eliminated data scenario had the highest median average catch during the recovery period because of the subset of simulated stocks that were estimated to be less depleted than the population in the operating model, resulting in more aggressive catch estimates from the estimation method (Table 3; Fig. 6, D–F). Additionally, the eliminated data scenario had the lowest median AAV during the rebuilding period (Table 3). The eliminated data scenario also resulted in the highest number of simulated stocks that never reached the target biomass (Table 2) as a result of incorrect parameter estimates at the start of the management period that resulted in catch estimates exceeding the harvest that would allow rebuilding within the population in the operating model (Table 3).

Estimation performance when survey data are also available

The estimates of spawning biomass (Fig. 7, A–C) and relative spawning biomass (Fig. 7, D and E) for the time-invariant case were median unbiased at the time of the first assessment in year 50. The addition of a survey index and composition data for all data scenarios led to less among-simulation variability and reduced median bias over the management period in relation to the simulations without survey data (Fig. 3, A–F). The presence of survey data when fishery data were eliminated (eliminated data scenario) allowed the majority of the simulated stocks to be estimated as rebuilt by the end of the management period (Fig. 7) compared with the large fraction of simulations in which the stocks failed to be estimated as rebuilt when only historical data were available from the fishery (Fig. 3). Similar to what was observed in the time-invariant case, reduced among-simulation variability in the estimates of spawning biomass and relative spawning biomass (not shown) were observed when the inclusion of survey data, in addition to fishery data when time-varying parameters were present.

The full data scenario had the lowest RMSE for relative spawning biomass during the early portion of the management period for both cases (time-invariant and time-varying), when the majority of simulations were estimated to be rebuilding for both cases (Fig. 8). However, midway through the management period, after a majority of the simulated stocks had rebuilt and data restrictions were removed, the data scenarios resulted in similar RMSEs (Fig. 8). The inclusion of survey data for all data scenarios resulted in similar estimates of the median number of years required to recover to the target biomass, and these estimates were similar to the median rebuilding time from the operating model.

Discussion

Maintaining fishery data at historical levels during rebuilding reduced the variation in estimates for spawning biomass, relative spawning biomass, and steepness

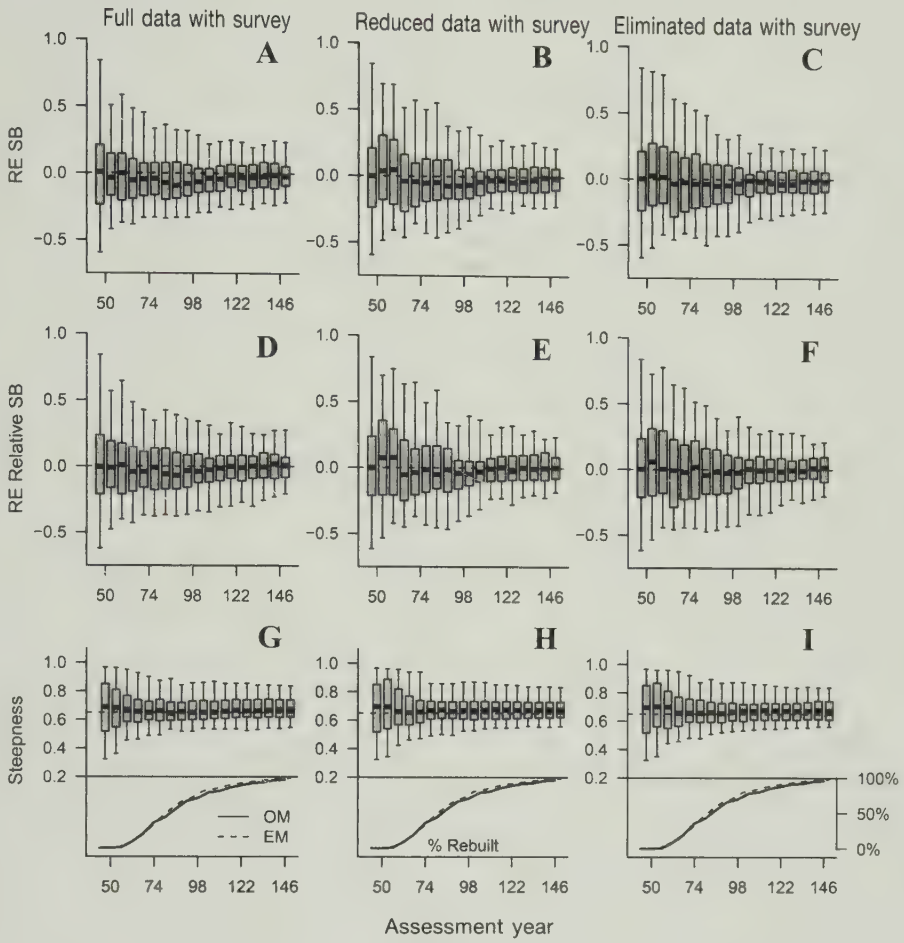

Figure 7

Relative error (RE) of estimated spawning biomass (SB) and relative SB and estimates of steepness in each assessment year when survey data are present during stock rebuilding for the time-invariant case and all 3 data scenarios (full data, reduced data, and eliminated data) for all simulations (top panels). The percentage of stocks that had rebuilt to the target biomass during the management period is shown in bottom panel within the operating model (OM, solid black line) and the estimation method (EM, dashed black line); data collection consequently returned to historical levels for the fishery when the EM determined that the stock was rebuilt. The black lines in the grey boxes denote the median of the estimates, the gray boxes cover the 25–75% simulation interval, and the boxplot whiskers cover the 95% simulation interval for each assessment year.

between assessments (i.e., over time within a simulation). Although the full data scenario had less variation, the median estimates of spawning biomass (over simulations) and relative spawning biomass were consistently below the operating model values for much of the management period. This result is contrary to what might be expected when additional data are available. Simulations in which there was a fishery-independent survey that provided an index of abundance and composition data (length and age) determined that this underestimation of the true spawning biomass was eliminated if survey composition data were available along with fishery composition data. The underestimation was driven by 2 key factors: the shape of fishery selectivity curve and data quantity. The specification of a fishery selectivity curve as greater than the maturity-at-length curve, with the fishery selecting only mature fish, resulted in a lag between recruitment to the population and recruitment to the fishery. However, conducting a fishery-independent survey that selects fish at smaller sizes yields information about recruitment to the population earlier than using data from the fishery that selects larger, mature fish. Additionally, an increase in the number of length- and age-composition

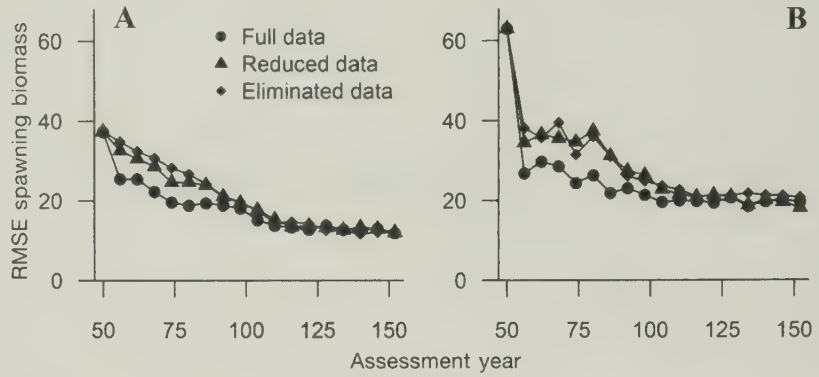

Figure 8

The root mean square error (RMSE) when survey data are available during rebuilding of a stock for relative spawning biomass in the assessment year for each case, (**A**) time invariant and (**B**) time varying, and data scenario (full data, reduced data, eliminated data).

samples from multiple data sources can improve estimates of recruitment, spawning biomass, and relative spawning biomass (Yin and Sampson, 2004; Wetzel and Punt, 2011).

The median relative errors for the relative spawning biomass were negative during the rebuilding period for the full data scenario and resulted in the estimation method failing to determine whether the population in the operating model was at, or above, the target biomass (median number of rebuilding years was greater than those in the operating model, Table 2). Failing to correctly determine that the population has rebuilt would lead to unwarranted extended harvest, a situation to avoid in fishery management. However, the reduced estimation variability (within and among simulations) offered by the full data scenario resulted in an improvement in the consistency of estimates by subsequent assessments, offering a level of stability for fisheries managers and stakeholders. In contrast, the higher between-assessment variation in estimates of spawning biomass for the reduced data scenario resulted in simulated stocks being estimated as rebuilt when the true population was still below the target biomass, a result that could have undesirable outcomes for fisheries management. Overly optimistic estimates of relative spawning biomass can result in overfishing when catch limits are set too high, leading to further reductions in biomass and potentially resulting in an overfished declaration based on a future assessment.

Loss of data during rebuilding resulted in a number of simulations that failed to estimate rebuilding because of poor initial estimates of steepness, a key parameter that controls how quickly a stock can rebuild from low biomass levels. In the absence of new data, the first and subsequent assessments were entirely dependent on the quality of the historical data to inform parameter estimates. The simulations that failed to correctly detect rebuilt stocks were driven by erroneously low estimates of steepness at the time of the first assessment. Therefore, initially identifying a stock as less productive than the true population resulted in lower estimates of spawning biomass and relative spawning biomass, and the assessment predicating harvest levels that were well below the true acceptable biological catch. The reduced harvest allowed the population in the operating model to rebuild to, or above, the target biomass. However, in the absence of new (and informative) data, the estimation method did not detect the correct simulated stock size. The population in the operating model had a 2-way trend of abundance (decline and increase in biomass) with the fishery data available during the fishing down and recovery periods, data that previous studies have found informative in estimating steepness (Magnusson and Hilborn, 2007; Conn et al., 2010). This work showed that a one-way trip scenario in stock size with limited data may not be adequate to correctly estimate steepness, but the inclusion of even limited data can, with a contrast in stock size, improve the estimation of steepness even if the initial assessment produced a poor estimate (Figs. 6C and 7).

The general trend in results when the operating model included time-varying natural mortality and fishery selectivity was similar to the trend in results for the time-invariant case, although the among-simulation estimates were more variable across all data scenarios. Natural mortality was fixed at a single value in the estimation method across all years equal to the mean value that was used to generate the autocorrelated annual deviations in the operating model. This setup was a strategic choice that allowed variation in the composition data that the estimation method would not be able to account for, but it was not anticipated to result in strongly biased estimates due to model misspecification. The processes that control natural mortality rates in real systems over the life span of an

individual are likely more complex with extended periods of high or low mortality that is affected by external factors (e.g., predator abundance, climate conditions)—periods that could result in large biases in estimated quantities if they are not accounted for in an assessment (Johnson et al., 2015).

Shifts in the form of selectivity over time and the impact of annual deviations in selectivity led to mixed results. The estimation method consistently overestimated the mean size at maximum selectivity for all data scenarios with time-varying selectivity. The operating model selectivity applied normally distributed deviations to generate the annual shifts in selectivity. One would not a priori predict the estimation method to have a consistent bias in estimates; however, the estimation method was able to identify the change in the selectivity form (asymptotic to dome-shaped through a reduction in the width at peak selectivity) during the rebuilding years with a similar error to that observed in the time-invariant case. Each case led to estimates that overestimated the width at maximum selectivity, the parameter defining the dome in selectivity (dome-shaped selectivity occurring at larger sizes with increased sizes subject to full selectivity compared with that in the operating model). Time blocks were applied within the estimation method defined by the status of the stock to allow shifts in selectivity, ignoring the annual deviations in the selectivity curve. Studies have evaluated other ways of estimating time-varying selectivity by using state-space models (Nielsen and Berg, 2014) or have examined the implications of applying time blocks versus allowing a random-walk component in selectivity parameters or catchability (Wilberg and Bence, 2006; Martell and Stewart, 2014). Further exploration should be conducted to determine whether allowing a random walk or applying an alternative estimation method eliminates the bias detected in the estimated selectivity observed here and how data quantity and quality affect these estimates. Additionally, if shifts in fishery selectivity are anticipated as a result of management actions, increased data collection may be required to achieve a similar level of precision in estimates of fishery selectivity during rebuilding.

As with other simulation studies, simplifying assumptions were used in this study and these can lead to an underestimation of the uncertainty that would be expected in a real-world population. With the estimation method used in this study, the population structure and functional form of biological relationships were assumed correctly—variables that are not known with certainty for a typical assessment. Additionally, the simulated composition data from the historical and management periods were representative of a homogenous population. In reality, one may expect spatial structure in fish populations, and, during a period of limited sampling, composition data may be available only from a subset of the population that may not be representative of the population as a whole. The results from this simulation study should be considered a best-case scenario specifically designed to allow clearer interpretation of the results regarding the availability of data for estimate rebuilding.

The work described here highlights the benefits of continued data collection during stock rebuilding on the precision of estimates, but there are many additional reasons why retaining data streams or creating new data streams are important. Data availability can fluctuate with harvest limits for species for which the fishery is the primary data source. Additionally, the data collected may be more variable because of variations in fishing behavior among fishermen, and the data typically will be available only for mature, larger animals selected by the fishery. The presence of consistent survey data for these stocks could improve the ability to produce a more robust estimate of stock status. Ideally, survey data would provide comparable data across time and space for a large portion of size and age classes for a population when it is collected by using standardized sampling protocols. Traditional trawl survey methods commonly used off the U.S. west coast have failed to capture sufficient samples for some rockfish species because of gear or area restrictions. Creating and maintaining alternative survey sampling methods (e.g., hook and line or underwater camera sampling) that sample representative portions of a stock would be one way to improve the assessment of certain rockfish species (e.g., Harms et al, 2008).

A benefit of continued data collection across multiple data sources is the potential ability to identify misspecification in model assumptions. With the estimation method and operating models applied in this study, similar structural assumptions were generally made. However, the true state of nature is never known with confidence and continued data collection may allow the identification of model misspecification in the structural assumptions (e.g., growth, recruitment), allowing models to better approximate reality. Specifically, there could be long-term changes in stock dynamics that are due to environmental conditions (e.g., Hollowed et al., 2011) or biological forces when a stock is depleted (e.g., Hixon et al., 2014; Legault and Palmer, 2016) that could negatively affect the ability of the stock to rebuild. In such a case additional data would be required to detect a lack of rebuilding despite reduced fishing mortality. Sampling during harvest restrictions will provide continued information that can identify changes in stock dynamics. Additionally, the creation of alternative data streams can buffer against the reliance upon a single and potentially variable data source and, in turn, could provide valuable insights into stock dynamics by the sampling of differing subsections of a population.

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Vertical distribution, diet, and reproduction of the velvet dogfish (*Zameus squamulosus*) in waters off Hawaii

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Abstract—The velvet dogfish (*Zameus squamulosus*) is a wide-ranging species of shark that is captured as bycatch in bottom and pelagic longline fisheries in the Atlantic, Pacific, and Indian oceans from near the surface to depths as great as 2000 m. Here we provide information on the vertical distribution, diet, and reproduction of the velvet dogfish based on examination of 21 specimens captured in Hawaiian longline fisheries. Only females (576–839 mm in total length [TL]) were captured in waters off Hawaii and this finding may indicate sexual segregation for this species. All individuals were captured in epipelagic and pelagic oceanic waters at estimated target hook depths between 24 and 400 m. Stomach and intestinal contents consisted of squid, fish, and shrimp. Females were immature at 576–729 mm TL and mature at 715–839 mm TL. Mature females contained 6–10 uterine eggs and 4–8 embryos. On the basis of results from a pregnant female (715 mm TL), the size of ovarian ova, and the width of the uteri of slightly larger individuals, female maturity was estimated to occur at 715–730 mm TL. No reproductive seasonality was detected; however, our sample size was small. Reproductive data from published records for size of near-term embryos and smallest free-swimming specimens with umbilical scars indicate that size at birth is 245–270 mm TL.

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The velvet dogfish (*Zameus squamulosus*) is a dark, nondescript shark species with a wide distribution along the margins of the Atlantic, Pacific, and Indian ocean basins and at a number of insular regions, including the Canary Islands, Hawaii, Japan, New Zealand, Okinawa, and Palau (Compagno, 1984; Taniuchi and Garrick, 1986; Yano and Kugai, 1993; Wetherbee and Crow, 1996; Pajuelo et al., 2010). Although this species was placed in the genus *Scymnodon* before the revision by Taniuchi and Garrick (1986), the genus *Zameus* is genetically distinct from *Scymnodon,* and *Zameus squamulosus* is recognized as the valid name for the velvet dogfish (White et al., 2014). This species occurs as bycatch in a variety of fisheries, including those using trawls and pelagic or bottom longlines (Krefft, 1980; Yano and Tanaka, 1984; Nakaya and Shirai, 1992; Pajuelo et al., 2010; Zhu et al., 2012; Romanov et al., 2013) at depths of 27–2000 m (Compagno, 1984; Last and Stevens, 1994).

Although the velvet dogfish has a wide distribution and is regularly captured, information about its basic life history remains fragmentary and has been hindered by misidentification. Not surprisingly, this species is categorized in the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species as data deficient (Burgess and Chin, 2006), and the limited information on its basic biology, which is required to assess the status of a stock or to evaluate fisheries impact on the population, is unavailable.

Few records exist on the diet and reproductive biology of the velvet dogfish. Compagno (1984) suggested that these sharks feed on bottom fishes and invertebrates, and Kobayashi (1986) reported an octopus

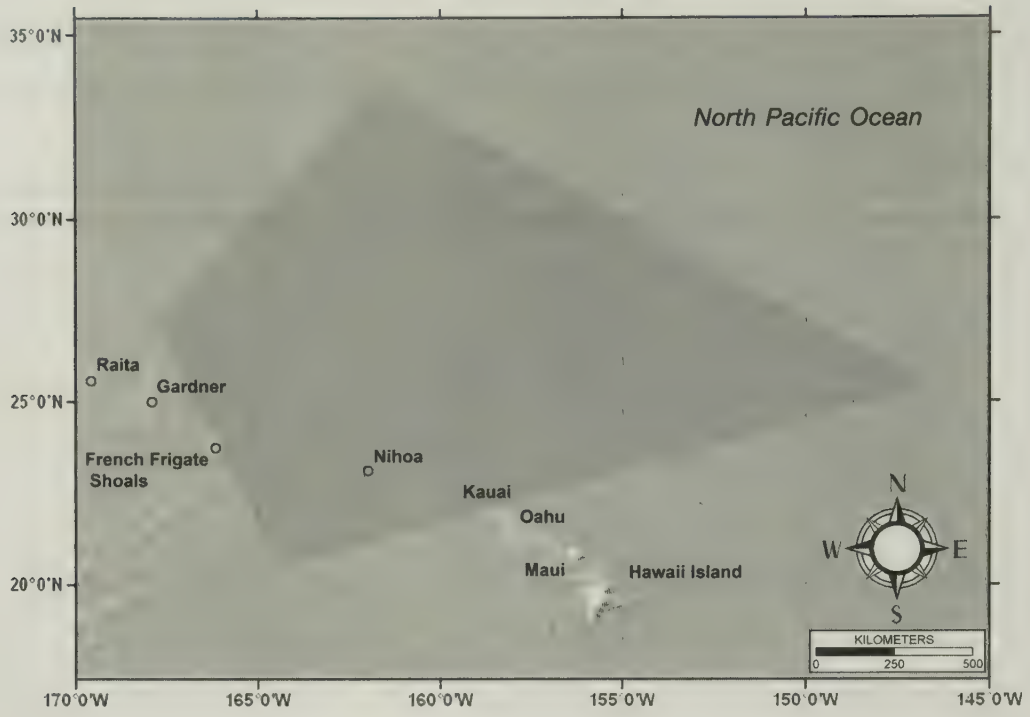

Figure 1

Map of the study area (darker shaded area) in the Hawaiian Archipelago, where velvet dogfish (*Zameus squamulosus*) were collected in Hawaii longline fisheries between 2001 and 2008 to determine their vertical distribution, diet, and reproductive stages.

in the stomach of one individual. On the basis of examination of a small number of reproductive tracts, velvet dogfish have been described as aplacental viviparous sharks that fit the type-II yolk-sac reproductive mode (in which several embryos with attached yolk sacs are contained in utero without uterine compartments) (Otake, 1990).

Male velvet dogfish are thought to mature between 493 and 522 mm in total length (TL) on the basis of clasper length and calcification of claspers (Krefft, 1980; Yano and Tanaka, 1984). Size at maturity for females is less certain. Melendez (1991) reported that females 510–551 mm TL were immature. Pajuelo et al. (2010) reported the smallest mature female at 571 mm TL, and Compagno et al. (2005) found mature females at sizes of 590–690 mm TL. However, Yano and Tanaka (1984) found that a 720-mm-TL female was immature and reported sizes between 750 and 840 mm TL for mature females. Brood size for velvet dogfish is not known, but Yano and Tanaka (1984) reported 3–10 ova in uteri of females, which may indicate that brood size falls within a similar range. Estimates of size at birth have spanned a large range, most likely attributable to misidentification. Ebert (2015) stated size at birth as 200 mm TL, and Cadenat and Blache (1981) reported free-swimming individuals as small as 246 mm TL. In contrast, Burgess and Chin (2006) reported sizes at birth of 68–90 mm TL. Individual velvet dogfish as large as 1094 mm TL have been noted (Pajuelo et al., 2010); the maximum size was previously reported as 840 mm TL (Yano and Tanaka, 1984).

Specimens of the velvet dogfish are occasionally captured in Hawaii longline fisheries that primarily target tuna species and swordfish (*Xiphias gladius*) (Walsh et al., 2009). Longlines that primarily target big eye tuna (*Thunnus obesus*) are typically set in the morning and hauled in the evening, and longlines that target swordfish are set in the evening and retrieved during the morning (Pooley, 1993; Pradhan and Leung, 2004). This fishery generally extends into the mid-North Pacific Ocean from the Equator to 40°N and between longitudes 145°W and 175°E (Pradhan et al., 2003) (Fig. 1). The capture of velvet dogfish as bycatch in the Hawaii pelagic longline fishery provided an opportunity to expand our knowledge about this species. We present information on the depth distribution, diet, and female reproductive biology of velvet dogfish captured in Hawaii pelagic longline fisheries.

Materials and methods

Vertical distribution

We examined 21 velvet dogfish from waters off Hawaii. Identification was based on the key provided in Compagno (1984) and on proportional and morphometric measurements of specimens in Wetherbee and Crow

(1996). Between 2001 and 2008, 19 specimens were collected through the Hawaii Longline Observer Program of the National Marine Fisheries Service, and these sharks were frozen on board the fishing vessels and retained for later examination. Two additional specimens captured by longline vessels were given directly to the authors by the fishermen of these longline vessels and were frozen until examined.

Estimated hook depth was based on target set depth designated by the boat captain for the deepest part of the longline and based on an approximation of individual hook positions on the longline. The median depth of the deepest hook on 266 deep sets (tuna sets) was 248 m, whereas data for 333 shallow sets (swordfish sets) indicated a median depth of 60 m (Bigelow et. al., 2006). Previous reports on data from temperature-and-depth recorders attached to longlines of fishing vessels in Hawaii indicated that about 70% of deep sets were close to targeted set depth (Bigelow et al., 2006). Therefore, records of hook depth of individual longline sets provide an estimated target depth for the capture of velvet dogfish.

Frozen specimens were thawed and measured for TL, which was measured with calipers to the nearest 0.1 mm; placing the shark on its side and its tail in the "natural" position, we measured in a straight line from the tip of the snout along the body axis to a point where a straight edge indicated a 90° angle to the body axis from the posterior caudal tip. The shark was then dissected, stomach and valvular intestine were examined for food contents, and its entire reproductive anatomy was examined.

Diet

The primary bait used with tuna longlines was Pacific saury (*Cololabis saira*), which can be recognized in the gut and excluded from a dietary analysis. Stomachs and valvular intestines were dissected carefully, and the contents were retained within a hand net made of a 800-μ fine mesh. Squid beaks, fish remains, and shrimp present in stomachs were preserved in 4–10% formalin for 3–10 d and then transferred to jars that contained 40–50% isopropanol for storage until analyzed under a dissection microscope and identified to the lowest recognizable taxa taxon. Squid beaks were identified by identified by a coauthor (RY).

Female reproductive biology

Reproductive tracts were examined to determine the stage of sexual maturity and reproductive status of specimens. Presence of ovarian ova, diameter and location of eggs, uterus width, and number of embryos were used to assess female reproductive biology. Ovarian ova, uterine ova, and uterine embryos were counted, and maximum ova diameter and uterine width were measured with calipers to the nearest 0.1 mm. The reproductive biology terms that we use were modified from that used by Tanaka et al. (1990) for the frill shark (*Chlamydoselachus anguineus*) and by Yano (1995) for the black dogfish (*Centroscyllium fabricii*). Sexual maturity was determined on the basis of the size of ovarian ova and uterine width. Females with ovarian ova diameters <10 mm and with thread-like uteri (<10 mm in width) were classified as immature. Females with both ovarian ova and uteri >10 mm were classified as mature. The reproductive classification that we used for mature females had 7 stages: 1) developing ova, nongravid, with developing ovarian ova and expanded uteri (>10 mm); 2) large ova nongravid, with ova and expanded uteri (>10 mm); 3) ovulating, with eggs in body cavity; 4) uterine ova, ova in the uteri after ovulation; 5) developing embryos, obvious embryos with yolk sacs in the uteri; 6) near-term embryos, uterine embryos that have absorbed their external yolk sac; and 7) postpartum stage: no uterine embryos and large flaccid uteri (>20 mm). Although no near-term embryos were observed in utero in velvet dogfish collected off Hawaii, size at birth was estimated from lengths of near-term embryos (Graham[1]; Romanov[2]) and size of the smallest free-swimming individuals (Graham[1]; Cadenat and Blache, 1981; Yano and Tanaka, 1984; Taniuchi and Garrick, 1986).

Results

Vertical distribution

All 21 velvet dogfish obtained from Hawaii longline fisheries were females. Estimated target depths of longline sets were between 24 and 400 m (median depth: 182 m [Table 1]). Females ranged in size from 576 to 839 mm TL. Specimens were captured within an area between 21–34°N and 148–168°W, and the majority of specimens were captured north of the Hawaiian Archipelago. The majority of sharks were captured on tuna longlines set in the morning between 0550 and 1144, timing that is characteristic of the deep-set tuna fishing method. An exception was a shark caught on a longline deployed at 1506. The deep-set tuna longline sets had a soak time of 6–11 h and typically were retrieved between 1505 and 2331 on the same day that they were deployed.

Diet

Nine of the 21 sharks examined had recognizable stomach or intestinal contents of mesopelagic and epipelagic prey (Table 2). Seven sharks contained squid beaks, squid eye lenses, and squid gladii. Fish remains (skin, eye lenses) were present in 4 sharks, and a shrimp

[1] Graham, A. 2016. Personal commun. Australian National Fish Collection, CSIRO, G.P.O. Box 1538, Hobart, Tasmania 7001, Australia.

[2] Romanov, E. 2016. Personal commun. Centre Technique d'Appui à la Péche ReUNionaise (CAP RUN), Darse de Pêche, Magasin 10, Port Ouest, 97420 Le Port, Île de Réunion, France.

Table 1

Capture records and reproductive biology for female velvet dogfish (*Zameus squamulosus*) collected from Hawaii longline fisheries between 1995 and 2008. The letters *a* and *b* indicate different velvet dogfish caught on the same longline set. N/A=not available.

ID no.	Capture date	Total length (mm)	Estimated hook depth (m)	Maturity status	Reproductive status
1	15 Oct 95	786	30	Mature	8 ovarian eggs; largest 37 mm; uterus width 18.5 mm
2	N/A	746	N/A	Mature	7 ovarian eggs; largest 52.8 mm
3	24 Sep 01	720	N/A	Mature	Uterine eggs; largest 47.9 mm
4	07 Oct 01	735	24	Mature	6 ovarian eggs; range 35.5–47.5 mm
5	12 Nov 01	758	400	Mature	9 ovarian eggs; range 44.4–56.5 mm
6	10 Nov 01	594	305	Immature	No sexual development
7	16 Dec 01	728	250	Immature	No sexual development
8	10 Feb 02	576	364	Immature	No sexual development
9	N/A	728	N/A	Mature	Uterine eggs not measured
10	28 Jul 02	752	110	Mature	Small ovarian eggs: largest 8.2 mm; uterus width 29–33 mm
11	26 Aug 02	791	180	Mature	4 embryos; range 31.4–36.7 mm TL
12	10 Sep 02	729	300	Immature	9 ovarian eggs: largest 34.4 mm; uterus width 8.6 mm
13	24 Mar 03	736	120	Mature	9 ovarian eggs; range 18.9–22.3 mm
14	23 Nov 08	805	N/A	Mature	8 uterine eggs (not measured)
15	08 May 08	715	83	Mature	8 embryos; range 44.5–60.4 mm TL
16	27 Apr 08	720	71	Mature	Ovary starting to develop; uterus width 10.5 mm
17	18 Aug 06	751	182	Mature	Ovary and uteri developed
18	28 Apr 08	722	82	Mature	Eggs ruptured in abdominal cavity
19	12 Nov 01	720	400	Mature	10 ovarian eggs; range 25.3–28.8 mm; uterus width 15.5 mm
20[a]	07 Jul 06	742	182	Mature	10 uterine eggs (not measured); uterus width 41.1 mm
21[b]	07 Jul 06	839	182	Mature	9 uterine eggs; range 38.5–47.7 mm

was present in 1 shark. Identifiable squid beaks represented 4 families; 2 identified species, *Nototodarus hawaiiensis* and *Sandalops melancholicus*; and 3 recognizable genera, *Histioteuthis*, *Onykia,* and *Walvisteuthis* (Table 2).

Female reproductive biology

Seventeen of the 21 examined velvet dogfish were mature. Both left and right ovaries of female velvet dogfish were functional. Uteri were noncompartmentalized and contained 6–10 ova that were between 36.7 and 52.8 mm in diameter. It is unclear whether all uterine eggs were fertilized. Four females between 576 and 729 mm TL had small, developing ovaries (<10 mm in diameter) and narrow uteri (<10 mm in width) and were classified as immature (Table 1). Seventeen females, ranging in size between 715 and 839 mm TL, had ova >10 mm in diameter and expanded uteri (>10 mm in width) and were classified as mature (Table 1). Six of the 7 stages of reproductive maturity for females were observed in the specimens from Hawaii. No near-term embryos were found. Large ova (>30 mm) were observed in ovaries of velvet dogfish captured during September, October, and November. The smallest pregnant female was 715 mm TL. Uterine eggs were observed in specimens collected during July, September, and November, and developing embryos were found in uteri of sharks obtained in May and August (Table 3). No reproductive seasonality could be detected from our limited sample size (Tables 1 and 3).

Brood sizes of 2 pregnant females were 4 and 8 embryos, and these ranged from 31.4 to 36.7 mm TL in August and between 45.5 and 60.4 mm TL in May. On the basis of the presence of yolk sacs and size of the embryos, we determined that none of them were considered near-term embryos.

Discussion

Vertical distribution

The capture of velvet dogfish in Hawaii pelagic longline fisheries, is not as rare an event as previously suggested (Wetherbee and Crow, 1996). The worldwide distribution of this species includes a number of insular locations, such as Hawaii, and other waters in the Pacific Ocean, the Atlantic Ocean, and the Indian Ocean, and indicates that this species is associated with islands in addition to continental slope habitats.

The estimated hooking depths for shark captures off Hawaii (24–400 m) and similar pelagic depths reported in other studies (Yano and Tanaka, 1984; Dai et al.,

Table 2

The dietary contents found in the stomachs (S) and valvular intestines (VI) of female velvet dogfish (*Zameus squamulosus*) captured in Hawaii longline fisheries between 1995 and 2008. Nine of the 21 sharks examined had recognizable dietary contents.

		No. of S and VI with dietary items	Total number of dietary items
Cephalopod			
Squid		7	20
	Nototodarus hawaiiensis	1	1
	Sandalops melancholicus	1	1
	Histioteuthis sp.	2	4
	Onykia sp.	1	1
	Walvisteuthis sp.	1	1
	Unidentified squid	4	12
Crustacean			
	Unidentified shrimp	1	1
Fish			
	Unidentified shark	1	1
	Unidentified teleost	4	4

Table 3

Number of female velvet dogfish (*Zameus squamulosus*), collected and retained each month from Hawaii longline fisheries between 1995 and 2008, classified as immature (IM) or in 1 of 7 stages of reproductive maturity: nongravid females with developing ovarian eggs (DO), nongravid females holding at least one large ovarian egg (LO), ovulating females (OV), postovulatory females with uterine ova (UO), gravid females carrying at least one encapsulated developing embryo (DE), gravid females carrying near-term embryos free in the uterus (NE), and postpartum females (PP). Table format is adapted from Tanaka et al. (1990) and Yano (1995).

Month	IM	DO	LO	OV	UO	DE	NE	PP	Total
Jan									0
Feb	1								1
Mar		1							1
Apr		1		1					2
May						1			1
Jun									0
Jul					2			1	3
Aug						1		1	2
Sep	1				1				2
Oct			2						2
Nov	1		1		2				4
Dec	1								1

2006; Zhu et al., 2012; Romanov et al., 2013) indicate that female velvet dogfish clearly exhibit an epipelagic aspect in their behavior. The capture of this species at depths as great as 2000 m also reveals a large vertical and benthic range in their movements (Pajuelo et al., 2010; Romanov et al., 2013). In general, larger squaloid sharks similar in size to velvet dogfish tend to be benthic, slope, or shelf dwellers, whereas the majority of oceanic dogfish species are smaller species (Hubbs et al., 1967; Pikitch et al., 2008). Female velvet dogfish regularly inhabit pelagic waters, and this relatively large squaloid may transition from bottom to midwater or pelagic waters to take advantage of feeding opportunities, probably by following migrations of midwater squid and fish (Parin, 1970; Krefft, 1980).

The capture of only females off Hawaii raises the possibility of sexual segregation, because females more frequently use the epipelagic environment and males remain more bottom oriented at greater depths. Sexual segregation for this species at other locations is indicated by the capture of only females on floating longlines in the northwestern North Pacific Ocean (Yano

and Tanaka, 1984) and a female:male ratio of 4.1:1.0 of velvet dogfish captured at the Canary Islands (Pajuelo et al., 2010). Segregation may result from the movement of females from depth to epipelagic water because a 1:1 sex ratio has been reported for velvet dogfish captured on bottom longlines at depths as great as 1000 m (Kobayashi, 1986; Nakaya and Shirai, 1992; Yano and Kugai, 1993). Sexual segregation has been reported for other members of the family Somniosidae, including the roughskin dogfish (*Centroscymnus owstonii*) and the Portuguese shark (*C. coelolepis*) (Yano and Tanaka, 1988; Girard and Du Buit, 1999), both of which are relatively large squaloid sharks.

Females captured in our study were mature or approaching maturity and therefore indicated that velvet dogfish may also segregate by size. Segregation may reflect the movement of mature females into epipelagic waters, and such movement may be related to reproduction rather than to feeding. There is evidence of segregation by size for a number of species of dogfish, including the closely related Japanese velvet dogfish (*Scymnodon ichiharai*): large individuals are thought to be more common inside the boundary of Suruga Bay, Japan, than smaller, immature individuals (Yano and Tanaka, 1984).

Diet

Our findings indicate that velvet dogfish feed primarily on squid and less on fish and shrimp; however, these results may be biased as a result of the longer retention of squid beaks in stomachs because of their resistance to digestion than the retention of other invertebrate prey or fish (Hyslop, 1980). The stomachs and intestines of females captured in the upper water column were examined for remains of prey and from an examination of these organs, squid appear to form the major portion of the diet. It is not surprising that squid are a major food item of the velvet dogfish in waters surrounding Hawaii, given the abundance of a number of species of squid that occur in this region. The greatest trawl catches for a wide range of cephalopod species in Hawaii have been recorded at night in the upper 200 m (Young, 1978). Many of these cephalopod species are thought to undergo a diel vertical migration from daytime depths of 400–700 m to shallower nighttime depths of 250–300 m (Young, 1978). The well-developed tail of velvet dogfish and the depth distribution of the various squid consumed by the dogfish examined indicate that the velvet dogfish may be an active feeder or an ambush predator in the epipelagic and mesopelagic zones. Active predation on pelagic cephalopods by adult and subadult Portuguese sharks in the Catalan Sea was also reported by Carrassón et al. (1992).

Female reproductive biology

Although the number of velvet dogfish specimens examined in our study was small, the information gained from our examination of these sharks expands our understanding of the reproductive biology of females of this species. Yano and Tanaka (1984) reported 3–10 ova in uteri of female velvet dogfish; however, actual brood size may be less in other squaloid sharks (i.e., 20–31 uterine ova and 16–28 embryos for the roughskin dogfish and 22–29 uterine ova and 15–29 embryos for the Portuguese shark) in Suruga Bay, Japan (Yano and Tanaka, 1988). The brood size for velvet dogfish examined in this study was 2–8 young. Five embryos 200–220 mm TL have been observed in the last third of the gestation period (Romanov et al., 2013; Graham[1]). Size at birth for velvet dogfish is estimated at 245–270 mm TL on the basis of observations of embryos with yolk sac attached at sizes of 200–220 mm TL (A. Graham[1]), free-swimming sharks 250–270 mm TL with faint umbilical scars (Graham[1]; Romanov[2]), and a 277-mm-TL free-swimming shark with an umbilical scar completely healed (Graham[1]). The minimum sizes reported for free-swimming individuals were 246–262 mm TL (Cadenat and Blache, 1981; Yano and Tanaka, 1984; Taniuchi and Garrick, 1986; Graham[1]). This information substantially narrows the range for estimates of size at birth from the large size (690 mm TL) previously reported by Burgess and Chin (2006) and the small size (200 mm TL) reported in Ebert (2015).

The estimated size at maturity for females was between 715 and 730 mm TL in our study and was based on the size of a 715-mm-TL pregnant female and immature individuals approaching 730 mm TL. These estimates reduce the size range at sexual maturity. Our estimate of size at maturity for females is substantially larger than the estimate of 590 mm TL reported by Compagno et al. (2005). Our current hypothesis is that there is no annual seasonal cycle of reproduction for this species; however, more data are required to confirm this notion. In waters off Hawaii, ovulating females and early-stage gravid females (small embryos 31.1–60.4 mm) were observed between April and August. Lack of a seasonal reproductive cycle is a common feature of squaloid sharks (Yano and Tanaka, 1984). The entirety of data available on reproduction in female velvet dogfish provides some evidence that they may be associated with the benthic habitat for parturition because of the capture of small, free-swimming individuals and females with near-term embryos in utero on bottom longlines (Romanov et al., 2013).

The velvet dogfish is an enigmatic species captured across a wide geographical range and throughout a range of depths in the water column. However, this species is rare in pelagic fisheries, and therefore it is typically caught in low numbers in fisheries around the world. For example, Dai et al. (2006) reported a catch per unit of effort (CPUE) for velvet dogfish of only 0.007 individuals/1000 hooks for longline fisheries in the eastern Pacific Ocean. In the Hawaii longline fisheries (swordfish and tuna longlines combined) during 1995–2006, the CPUE of velvet dogfish was 0.005/1000 hooks (Walsh et al., 2009). In the eastern central Pacific Ocean, velvet dogfish were caught primarily at a median depth of 190 m, and the box plot of 25 and

75 percentiles was in a range of 165–210 m (Zhu et al., 2012). This range is similar to the median depth of 248 m reported for the tuna longline fishery in the Hawaiian Islands (Bigelow et al., 2006). The CPUE for velvet dogfish in Hawaii likely would be slightly higher if only tuna longlines were considered.

There is some evidence that bycatch of velvet dogfish in commercial fisheries is increasing. Romanov et al. (2013) reported increased numbers of velvet dogfish caught in pelagic fisheries in the Indian Ocean since 1989, but this species was not reported as bycatch in this fishery from 1961 to 1989. They suggested that increased abundance of velvet dogfish and other mid-size oceanic predators in pelagic fisheries may be related to broad ecological shifts in oceanic waters that have occurred over the past few decades. Polovina et al. (2009) suggested that recent increases in abundance of other mid-size mesopredators, including bramids (pomfrets) and gempylids (snake mackerels) in pelagic fisheries operating from Hawaii may be attributed to a reduction in apex predators in this ecosystem. The increasing presence of velvet dogfish in the bycatch of pelagic fisheries may be a harbinger of a shift that will occur in these fisheries. The ecological position and population dynamics of mesopredators and their link to fisheries are important considerations for the management of these species.

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Fishery Bulletin

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Articles generally range from 20 to 30 double-spaced typed pages (12-point font) and describe an original contribution to fisheries science, engineering, or economics. Tables and figures are not included in this page count, but the number of figures should not exceed one figure for every four pages of text. Articles contain the following divisions: abstract, introduction, methods, results, and discussion.

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lished by the Council of Science Editors. For scientific nomenclature, use the current edition of the American Fisheries Society's *Common and Scientific Names of Fishes from the United States, Canada, and Mexico* and its companion volumes (*Decapod Crustaceans, Mollusks, Cnidaria and Ctenophora*, and *World Fishes Important to North Americans*). For species not found in the above mentioned AFS publications and for more recent changes in nomenclature, use the Integrated Taxonomic Information System (ITIS) (available at website), or, secondarily, the California Academy of Sciences *Catalog of Fishes* (available at website) for species names not included in ITIS. Common (vernacular) names of species should be lowercase. Citations must be given of taxonomic references used for the identification of specimens. For example, "Fishes were identified according to Collette and Klein-MacPhee (2002); sponges were identified according to Stone et al. (2011)."

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Word usage and grammar that may be useful are the following:

- *Aging*
  For our journal, the word *aging* is used to mean both age determination and the aging process (senescence). Authors should make clear which meaning is intended where ambiguity may arise.

- *Fish and fishes*
  The plural of the word fish (a collective noun that implies individuals without regard to species) is *fish*.
  Example: The *fish* were collected by trawl net.
  Example: The numbers of *fish* collected that season were less than the numbers from previous years.

  The plural for *fish species* is *fishes* (a contrived plural used by taxonomists to mean several or more *fish species*) or one can use *fish species* (which is preferred in this journal for clarity across disciplines).
  Example: The *fishes* of Puget Sound [biodiversity is implied] or
  The *fish species* of Puget Sound [preferred plural for clarity across disciplines].

- *Crab and crabs, squid and squids, etc.*
  The plural of the word *crab* (i.e., many individuals without regard to species) is *crab*.
  Example: The crab were sorted by weight.
  Example: Many red king *crab* were dying [Many individuals of one species of crab.]

  The plural of *crab species* is *crabs* (a word used by taxonomists) or *crab species* (the latter is preferred in this journal for clarity).
  Example: These *crabs* were selected for treatment. [Different crab species are implied.]
  These *crab species* were selected for treatment. [Preferred word choice for clarity of meaning.]
  Example: Snow *crabs* are found throughout the North Pacific Ocean and Bering Sea. [There are 2 species of snow crab and therefore the word *crabs* can be used here.]
  Two species of snow *crab* are found throughout the North Pacific Ocean and Bering Sea. [Preferred usage for clarity.]
  Example: Three crabs were selected for treatment. [3 species of crab are implied.]
  Three crab species were selected for treatment. [Preferred word choice for clarity.]

- *The definite article with common names of species*
  When the singular common name of a species represents the entire class or group to which it belongs, use the definite article.
  Example: Only one species of the genus Salmo is found in the Atlantic Ocean—*the* Atlantic salmon (*Salmo salar*).
  Example: The sonic emissions of *the* bottlenose dolphin are complex.

  For plural common names, this rule does not apply.
  Example: Chinook salmon are found throughout the Pacific Ocean.
  Example: Bottlenose dolphins are found in temperate and tropical waters.

- *Sex* For the meaning of male and female, use the word *sex*, not *gender*.

- *Participles* As adjectives, participles must modify a specific noun or pronoun.
  Example: Using mark-recapture methods, these scientists determined the size of the population. [Correct. The participle *using* modifies the word *scientists*.]
  Example: These scientists, based on the collected data, concluded that the mortality rate of these fish had increased. [Incorrect. The scientists were not based on the collected data.]
  These scientists concluded, on the basis of collected data, that the mortality rate of these fish had increased. [Correct. The offending participle has been eliminated and an adverbial phrase modifies the verb *concluded*.]

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